A study of the growth and fertility of different beef cattle genotypes in a tropical environment with implications for the genetic improvement of productivity.

Thesis submitted by

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ABSTRACT

One method of improving the genetic performance of beef cattle in any environment is to select for improved growth and fertility using Estimated Breeding Values (EBV's) to identify the superior animals. Improving the accuracy of these EBV's requires the use of datasets and models that are appropriate to that environment.

A study of the growth and fertility of beef cattle from a dry tropical environment was undertaken using data from CSIRO's National Cattle Breeding Station, "Belmont" (23°S, 150°E). The data were collected from 1974 to 1990 from Hereford-Shorthorns (HS), Brahman x HS (BX) and low (BL) and high (BH) grade Brahmans. Components of the models of growth and fertility were analysed using a least-squares analysis of variance.

The dependent variables that described growth were calf day of birth (CBDAY) and the growth variables of birth weight (BWT), and age-adjusted weights at a 200 day weaning weight (WWT), 365 day yearling weight (YWT) and a 550 day final weight (FWT). The dependent variables that described female fertility were pregnancy success, the heifer's day of birth (HBDAY), cow liveweight at the start of the breeding season (IWT), cow weight gain per day during the breeding season (MWGD) and the day of calving (DAYOC).

Environmental category, genotype and the combined effects of cow age and previous lactational status (AGEPLS) were used as fixed effects for both growth and fertility. If the BWT of a calf crop was above the overall mean for BWT, the calf crop was assigned to a "good" years (low stress) environmental category and if the BWT was below the overall mean BWT, the calf crop was assigned to a "poor" years (high stress) environmental category. This procedure was repeated for WWT, YWT and FWT. Environmental categories of "good", "average" and "poor" years were based on pregnancy rate and were used in the analysis of all fertility variables. The relative

performance of the genotypes was explained in terms of production potential (i.e. growth and fertility able to be achieved when environmental stress is negligible) and resistance to environmental stress. The production potential of the BL was less than the HS, similar to BX but higher than that of the BH. The productivity in the environments of relatively high stress was least for HS, intermediate for BX and highest for BL and BH. Whereas 3 year old maidens achieved relatively high pregnancy rates their calves were associated with the lowest growth rates. Lactating cows, especially young lactating cows, had lower productivity than non-lactating cows. The 5+ year old non-lactating cows were consistently the most productive class of AGEPLS. For lactating cows, HS (70.9%) were more fertile than both BX (59.9%) and BL (61.1%) which were more fertile than BH (49.9%). For 3 year old maidens and non-lactating cows the genotypes ranked in a similar order but the differences were small. Sex of calf was a significant effect for growth but not for fertility. Compared to female calves, male calves were born later, heavier and maintained higher rates of growth.

Interactions between genotype and environmental category were also explained in terms of production potential and resistance to environmental stress. The interaction between genotype and AGEPLS for growth was only significant for WWT and the AGEPLS effect on calves was reduced as the Brahman content increased. For pregnancy rate, the AGEPLS effect on HS was minor compared to the effect on the BH. Of the four growth variables, the interaction between AGEPLS and environmental category was only significant for FWT. The effect of AGEPLS on FWT in good years was minor compared to the effect in poor years.

The time-of-calving variables were significant covariates in the analysis of both growth (CBDAY) and fertility (HBDAY and DAYOC). IWT and MWGD were significant positive regressions for fertility but IWT was shown to be more important than MWGD. Increasing the IWT of heifers would increase their reproductive rate but this increase would be greater in the BH

than in the other genotypes. Increasing the IWT of lactating cows would also increase their reproductive rate but the response would be greatest in the poor years and least in the good years.

Components of the models were discussed with relevance to constructing models of growth and fertility that can be used in genetic improvement programs for northern Australia.

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DECLARATION

I declare that the work described in this thesis is entirely my own and has not previously been submitted in any other form at any other university, institution or tertiary education centre for the award of a higher degree. The information derived from the published or unpublished work of any other person has been acknowledged.

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C.J. O'Neill
March 1995

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DEDICATION

To my wife, Heather, and my two sons, Sean and Darsy, for their understanding and perseverance.

CHAPTER 1

INTRODUCTION

Improving the efficiency of beef production at any location can be achieved by simultaneously improving the environment and the genetic performance of cattle. Whereas the first strategy can involve substantial and continuous inputs of capital, equipment and biochemical technology, the second strategy involves relatively low investment in capital and equipment, is sustainable and is not harmful to the environment. Historically, both of these strategies have been pursued more vigorously in temperate regions compared to tropical regions.

This can be illustrated by dividing worldwide beef production into geographical regions. In 1980, the kilograms of carcass produced per beast per year were 87, 80 and 59 kg for North America, Europe and Oceania respectively, whereas the corresponding values for South America, Africa and Asia were 32, 17 and 10 kg respectively (Jasiorowski, 1983). The differences in this measure of productivity are related to differences in the systems of beef production, genotypes and environmental factors, such as climate, parasites and diseases. As pointed out by Hunter and Buck (1992), the regions that have achieved high levels of productivity are those with favourable environments and production systems that incorporate a high input of capital expenditure to improve the production environment, via nutrition, housing, and control of parasites and diseases. Furthermore, these regions make full use of the available genetic technology to improve the genetic performance of cattle (Wray *et al.*, 1991). Conversely, regions of low productivity are usually associated with relatively high and variable levels of environmental stress and low inputs and capital expenditure. Generally the levels of research and development of genetic technology are also low and the limited research that has been undertaken has had only partial acceptance by the beef industries in these regions (for northern Australia see O'Rourke *et al.*, 1992).

The Australian component of the geographical region of Oceania can be further divided into sub-regions of southern Australia and northern Australia. In southern Australia, the production systems, environments and genotypes are comparable to those of North America and Europe. On the other hand, in the tropical and sub-tropical environments of Australia the production systems and genotypes are similar to those in tropical South America and Africa.

Until recently, programs chosen to genetically improve cattle in southern Australia have primarily focussed on within-breed selection. In 1985, the Agricultural Business Research Institute (ABRI), of the University of New England, introduced BREEDPLAN as a within-herd genetic evaluation system for Australia's National Beef Recording System (NBRS) (Nicol *et al.*, 1985). BREEDPLAN uses mixed linear model (fixed and random effects) methodology (Henderson, 1973) to compute an estimated breeding value (EBV) for a particular trait for each animal based on the performance of that individual, its progeny and close relatives. The crossing of breeds within *Bos taurus* has now gained general industry acceptance and the Animal Genetics and Breeding Unit (AGBU) of the university is also investigating the use of mixed model methodology to genetically improve herds in crossbreeding programs.

The essential problem for genetic improvement programs, within a genotype, is to separate genetic from environmental variation (Falconer, 1989). Mixed model methodology separates these two components by simultaneously estimating constants for the environmental fixed effects (e.g. age of dam) and the random values (breeding values of individual animals) (see Bichard, 1990; Meyer, 1990; van Raden, 1990; Schneeberger, 1992). An additional source of environmental variation is the differential treatment of animals (e.g. different feeding levels) and thus different management groups must also be identified as environmental variation. The rate of genetic improvement obtained from using EBV's as a selection tool depends upon the accuracy of the estimation of the breeding value, where accuracy is defined as the correlation between EBV and the true breeding value (see Tier *et al.*, 1991 and Kinghorn, 1992). If the estimation of the genetic parameters (heritabilities, additive genetic variances, covariances, correlations) are poor then the corresponding estimation of breeding values will also be poor (Johnson and Garrick, 1990; Thompson, 1989). AGBU continues efforts to improve their methods of genetic evaluation (Oikawa *et al.*, 1991; Sivarajasingam *et al.*, 1991).

Hammond (1989) defines three primary components of a genetic improvement program, viz:

1. Breeding objective - a breeding objective aims to improve the economic efficiency of the herd.
2. Genetic evaluation - data on a trait that meets this objective, as well as information on all the factors contributing to the environmental variation associated with the trait, are compiled into a dataset. A genetic evaluation model is then constructed. This consists of nominating the target trait as the dependent variable and the environmental variation being partitioned into components of fixed effects, management groups, interactions and covariates. Based on this model, the mixed model methodology is used to generate genetic parameters, genetic trends and EBV's for the trait.
3. Breeding program design - the trait is improved by selecting replacement sires, culling cows and selecting mating pairs on the basis of their EBV's.

The mixed model methodology is also used in northern Australia. However, the genetic parameters and models currently used by AGBU to generate EBV's were derived from very few studies actually conducted in the tropics. If the genetic strategies of southern Australia are to be successfully applied to northern Australia, genetic improvement programs will need to use estimates of genetic parameters derived from suitable data and to use genetic prediction models that accurately describe the underlying biology of beef production in the northern environment. Hence, the literature on the major components of genetic evaluation models for both temperate and tropical environments, are compared and contrasted because the evidence suggests that datasets and models of growth and fertility are not interchangeable between the two environments.

1.1 Components of a genetic evaluation model : Dependent variables

The initial step in the construction of appropriate models for both growth and fertility is to choose dependent variables that accurately describe the growth and fertility of a herd in a particular environment. The fertility of females and the growth performance of calves are taken as basic elements of on-farm productivity, as on-farm productivity is defined as the average weight of beef produced per cow in the breeding herd.

The generally accepted procedure to genetically improve the growth rate of cattle is to select for high growth rate itself. However, this selection procedure may be inadequate. The study of correlated responses in cattle by Frisch (1981) and the reviews by Barlow (1978) and Baker and Morris (1984), of liveweight selection experiments from both temperate and tropical regions, highlight some important inconsistencies for such a selection procedure. These inconsistencies are associated with correlated responses in dystocia, milk production, female reproduction, resistance to environmental stress and growth potential (where growth potential is defined as the growth achieved in the absence of environmental stress). Because of these correlated responses, the present review will concentrate on the growth traits that are associated with key events in the on-farm production cycle, i.e. birth, weaning and calf ages at 12 and 18 months. The liveweights of calves at these ages then form the traits of interest for genetic improvement and as such the traits become the dependent variables for genetic evaluation models.

1.1.1 Birth weight

The weight of a calf at birth, that is either extremely high or low, is related to reduced productivity (Laster *et al.*, 1973; Bellows and Short, 1978; Morris *et al.*, 1986; Newman and Deland, 1991; Turner and Farnsworth, 1993 and see review by Meijering, 1984). Furthermore, as the cow's uterine environment can be regarded as a benign environment, the calf's birth weight (BWT) is an indication of growth potential (Frisch, 1981) and consequently, there can be a correlated response of an increased BWT from selection of high growth rates at all other ages (see reviews by Koch *et al.*, 1982 and Baker and Morris, 1984). As pointed out by Naazie *et al.* (1989), from studies in temperate regions, both crossbreeding to continental *Bos taurus* and selection of sires based on high growth performance, have often increased BWT's without a corresponding increase in the mature size of the cows.

Whether findings from temperate regions can be directly transfered to tropical regions remains to be fully evaluated. Work by Frisch (1981) and Burrow *et al.* (1991) has shown that selection for high weight per age does not necessarily result in an increase in BWT. Frisch (1981) noted that in a hostile environment, for a genotype with low resistance to environmental stress, selection for high growth rate can be equivalent to selection for resistance to environmental stress and not necessarily growth potential and hence, BWT will not increase as a correlated response. However, the early evidence of recent selection and crossbreeding experiments on "Belmont" (Frisch *et al.*, unpublished) indicate that high birth weights and dystocia are important issues in genetic improvement programs in the tropics. Hence, BWT must be continually monitored as a correlated response in any population involved in a genetic improvement program for growth.

1.1.2 Weaning weight

The weaning weight of a calf not only provides a measure of the calf's ability to grow (i.e. its growth potential and resistance to environmental stress) but also a measure of the maternal environment provided by the dam (Willham, 1972). The high correlations between milk production of the dam, and the pre-weaning growth rate of the calf (see Koch, 1972) have important implications for genetic improvement programs particularly in the tropics.

Indeed, the implications for genetic improvement programs are critical for the dry tropics, a region in which environmental stress, particularly nutritional stress, can be both extremely high and variable. If either the growth potential and/or level of resistance in the calf is increased (i.e. either by selection for high growth rate or by heterosis) and the weaning weight of the calf is increased there will be a corresponding increase in the demand for milk. Increasing the milk supply to meet this demand will adversely impact on the liveweight and condition of the cow. The adverse effects on cow liveweight and condition have a corresponding adverse effect on the cow's ability to rebreed whilst still lactating (Frisch *et al.*, 1987; see review by Galina and Arthur, 1989c). If the genetic antagonism between high milk production and fertility (see Hansen *et al.*, 1983; Oltenacu *et al.*,1991) is substantial, weaning weight becomes a critical parameter for genetic evaluation models of growth in tropical environments.

1.1.3 Post-weaning weights

The choice of post-weaning traits of growth is mainly determined by the choice of market being targeted by the beef producers. Whereas in temperate environments *Bos taurus* cattle are marketed at 6 to 36 months of age, in tropical environments, *Bos indicus* (ie mainly Brahman and Brahman derived) cattle are marketed from 2 to 5 years of age. To accommodate these differences, the genetic evaluation systems for growth traits are being developed in different directions. In 1991, AGBU introduced the third generation of BREEDPLAN (within herd) and GROUP BREEDPLAN (between herd). This generation of BREEDPLAN consisted of "BREEDPLAN 600" for temperate breeds, with an analysis of birth weight and liveweights at 200, 400 and 600 days, and "BREEDPLAN 900" for tropical breeds with an analysis of liveweights at 200, 550, 700 and 900 days (Schneeberger *et.al.* 1991). However, the 1994 analysis of GROUP BREEDPLAN for Brahmans consisted of a 200, 400 and 600 day weights (Anonymous 1994) and did not use weights at either 550, 700 or 900 days.

1.1.4 Female reproductive traits

Female reproductive traits that could be used for models of genetic evaluation include; pregnancy success - a positive or negative pregnancy result at the time of pregnancy diagnosis; calving success - whether or not a cow produces a calf from a defined breeding season; weaning success - whether or not a cow weans a calf from a defined breeding season; number of calves - total number of calves over the lifetime of a cow; days to calving - number of days between beginning of joining and day of calving; calving interval - number of days between day of calving of successive calves; calving date - date of calving as a numerical day of the year. The trait, days to calving, was identified by Meyer *et al.* (1990) as most suitable as the dependent variable for the models of genetic evaluation for fertility. Days to calving is now the recommended trait for fertility EBV's that are to be generated by BREEDPLAN for both southern and northern Australia (Schneeberger *et al.*, 1991). However, Davis (1993) and Frisch (1993) have rightly voiced reservations about the selection of this trait in the production systems of northern Australia. In northern Australia, in some years, half of the herd are non-calvers (Frisch *et al.*, 1987) and replacement females are purchased to maintain breeder numbers (Entwistle, 1984). Frisch (1993) makes the point that calving rate has similar heritability (h^2) to days to calving and questions the suitability of assigning a days to calving value to non-calvers when the non-calvers constitute a large proportion of cows. Davis (1993) also contends that because breeding seasons in the north are often extended to all year round, either calving success or number of calves over a lifetime may be more useful indicators of cow reproductive performance than days to calving.

1.2 Management groups

To construct appropriate datasets and models for a particular environment, due consideration must be given to the system by which beef is produced. Very little research has focused on the effect of the various production systems on the generation of genetic parameters and EBV's. It is necessary to define the production system from which the data and models are derived and allocate each factor that affects growth and fertility as either a separate management group or fixed effect. The main factors used to define the production system of cattle are as follows; methods of growing cattle, age at first breeding season, timing of breeding season, and strategies involving the management of calves.

1.2.1 Methods of growing cattle

The post-weaning systems in tropical regions compared with those of temperate regions are vastly different. In temperate regions, in general, all castrated male weaners enter a feedlot. The genotype is normally *Bos taurus* and environmental effects are greatly reduced or eliminated. In tropical environments, the corresponding males usually have some *Bos indicus* content and are generally grown on pasture where environmental stress can be relatively high. In other production systems of the tropics, cattle are initially grown on pasture but then finished to market weight on forage or in feedlot. Cattle grown on pasture can then be subjected to various strategies of parasite control.

The different strategies for growing cattle may directly influence the successfulness of a genetic improvement program for growth rate. As noted by Baker *et al.* (1991), the impact on genetic parameters is relatively unknown as very few studies have assessed genetic parameters for the same trait in different production systems. Itulya *et al.* (1987,p.1635) state: "...that genes favourable for high growth rates in a good nutritional environment favour enhanced cellular metabolic processes whereas these same cellular mechanisms would result in greater weight loss in a limited or stressful nutritional environment". The authors question the selection of replacement animals based on EBV's calculated from genetic parameters derived in a favourable environment (e.g. supplementary feeding) as this may decrease the fitness of a herd when exposed to an unfavourable environment (e.g. semi-arid rangelands).

1.2.2 Age at first breeding

Female calves reared in temperate or in tropical environments are subjected to two distinct production systems. The post-weaning growth rates of heifers in temperate environments are such that they normally enter the breeding herd as yearlings (Pinney *et al.*, 1972; Notter, 1988). In tropical environments, because of the lower growth rates in this environment, heifers are normally managed to enter the breeding herd at 2 years of age (Rudder *et al.*, 1982a; Taylor and Rudder, 1984; see review by Galina and Arthur, 1989a).

1.2.3 Timing of breeding season

In both temperate and tropical environments the breeding season and calving season can be restricted to take advantage of the most favourable environments. In temperate regions of North America, Europe and Australia there is usually a fixed breeding season of 60 to 90 days and most cows (about 80%) calve on an annual basis (BIF, 1981; Dzuik and Bellows, 1983; Reid, 1990; Deutscher *et al.*, 1991). In contrast, the breeding seasons of northern Australia and the other tropical regions, can vary from 3 months to all year round and yearly calving percentages may fall to as low as 40 to 50% (Galina and Arthur, 1989b; Reid, 1990). In northern Australia, the incidence of reproductive diseases such as vibriosis and trichomoniasis which delay conception, can remain undetected in a herd with an all-year round breeding season and thus contribute to lower reproductive rates (Andrews, 1976).

1.2.4 Calf management strategies

Worldwide, management strategies of calves are also being investigated as a means by which fertility can be increased. In northern Australia, the strategies include early weaning of calves (less than or equal to 150 days of age) (Boorman and Hosegood, 1986; Schlink *et al.*, 1988), and creep feeding (i.e. feeding supplements to calves while being nursed) (Schlink *et al.*, 1988). These strategies are aimed at improving both the survival and fertility of lactating cows. In northern Australia and elsewhere, both strategies increase the cow's body weight and fertility by removing the stress of lactation (Laster *et al*, 1973a; Ray *et al.*, 1975; Moore and da Rocha, 1983; Lusby *et al.*, 1981). In addition, early weaning decreases the interval between parturition and resumption of oestrus by also removing the sucking stimulus (Short *et al.*, 1972; Wettemann *et al.*, 1978; Carruthers *et al.*, 1980; Bluntzer *et al.*, 1989).

Calf management strategies would normally be regarded as different management groups in genetic prediction models for fertility. Nevertheless, it is conceivable that genes responsible for high fertility in an early weaning system would be different from the corresponding genes in a late weaning system. Cows that are prone to post-partum anoestrus are weaned early (e.g. 100 days). Hence, cows with genes for these traits are now able to rebreed, simply because of the production system. However, the same cows in a late weaning system (e.g. 200 days) would remain anoestrus for the duration of the breeding season. In this system the cows that do rebreed have a genetic make-up that either over-rides or does not display anoestrus from the effects of lactating and/or sucking stimulus. It follows that animals with high EBV's for fertility in an early weaning system will be unlikely to display that high fertility in a late weaning system. Hence the procedure of allocating cows from different weaning times into separate management groups, for the genetic evaluation of fertility may be inappropriate. This suggests that genetic evaluation of herds in which early weaning is practiced should be run separately to herds in which late weaning is practiced.

1.3 Fixed effects

One of the major reasons for the differences in regional productivity is the type of environment in which the cattle are reared. Unlike temperate environments, tropical environments are characterised by extremes of rainfall and temperature, which in turn, have an influence on soils, the availability and quality of forage, and the prevalence of parasites and diseases (see Webster and Wilson, 1980). Of the multitude of parasites and diseases found in the tropics, some can be highly stressful and/or fatal to cattle (see Hall, 1985). In both temperate and tropical environments the combined effects of all these factors are manifested as the effect of years-seasons. Hence, the current use of mixed model methodology removes the variation in growth and fertility due to these factors as the fixed effect of years-seasons. However, in tropical environments extreme variability between years and seasons may also need to be taken into consideration. In addition to the effects of years-seasons, the effects of the maternal environment, sex of calf and genotype also need to be considered in the temperate versus tropical environment.

1.3.1 Years

Growth

In temperate environments the small but significant differences in growth between years are well documented (e.g. Brown, 1960; Damon *et al.*, 1961; Bourdon and Brinks, 1982; Dinkel et al., 1990). In tropical environments, the effect of different years on growth has also been shown to be significant (e.g. Kennedy and Chirchir, 1971; Lapworth *et al.*, 1976; Rudder *et al.*, 1982b; Ahunu *et al.*, 1993; Fordyce *et al.* 1993a,b) but the extent of the variation is dependent on location. An indication of the extent of this variability is illustrated by studies of weaning weight from the wet tropics of central Africa and the dry tropics of northern Australia. Over 18 years, the yearly range in 205 day weaning weights of West African Shorthorn crossbreds of Ghana (latitude 7° N) was 75 to 141 kg (Ahunu *et al.*, 1993). Over 5 years, the Australian National Cattle Breeding Station "Belmont", (latitude 23° S) the variation in 253 day weaning weights of Africander, Brahman and British calves, ranged from 161 kg to 195 kg (Kennedy and Chirchir, 1971). By contrast, in the 5 year study of 180 day weaning weights of Angus, Brahman, Brangus and Hereford calves from the sub-tropical environment of Louisiana (latitude 32° N) the yearly weaning weights ranged from 186 kg to 196 kg (Damon *et al.*, 1961). At the lower latitudes the values of weaning weight are relatively low and the range in values is greater.

Fertility

In both temperate and tropical environments, the differences in fertility between years have been shown to be significant, but in the tropics the differences are much greater. In temperate environments, studies that have shown small differences include those by Dearborn *et al.* (1973), Buddenberg *et al.*, (1989) and Rahnefeld *et al.*, (1991). Numerous studies in tropical and sub-tropical environments have shown the effect of years to be both significant and large (Deese and Koger, 1967; Seebeck, 1973; Madalena and Hinojosa, 1976; Frisch *et al.*, 1987; Mackinnon, 1988; Haile-Mariam and Kassa-Mersha, 1994).

Tropical regions can undergo periods of drought for a year or more. Drought can result in not only dramatically reduced rates of pregnancy but also significantly high levels of both cow and calf mortality. In a study of 802 *Bos indicus* cross cows in the drought of 1982-83 in northern Australia (latitude 20°S), 21% of the cows died and 31% of the calves were lost between confirmed pregnancy and weaning (Fordyce *et al.*, 1990). By comparison, the magnitude of the variability in temperate regions is relatively small.

1.3.2 Seasons

Growth

In temperate environments, the differences in growth can be highly significant between seasons (e.g. Brown, 1960; Bolton *et al.*, 1987a,b; Winroth, 1990; McCarter *et al.*, 1990,1991a,b). Calves that have been born in autumn/winter are usually significantly disadvantaged over calves born in spring/summer (Bourdon and Brinks, 1982; Bolton *et al.*, 1987a,b; McCarter *et al.*, 1990, 1991b). McCarter *et al.* (1991a) found that cows calving in spring had a typical lactation curve, whereas for cows calving in autumn, yield of milk was highly variable.

In tropical environments the highly significant effect of seasons is also well documented for all growth traits from birth weight to carcass weight (Wheat, 1970; Gomez *et al.*, 1974; Iloeje, 1986; Taylor *et al.*, 1991). Seasons are partitioned on the basis of rainfall and are categorised into "wet" (high rainfall/summmer) and "dry" (low rainfall/winter-spring). The beef systems of the tropics are usually relatively productive during the "wet" season when both rainfall and ambient temperature are high and the availability of forage is greatest. On the other hand, the "dry" season is characterised by very poor growth rates of cattle (see Hunter, 1991 and Hunter and Buck, 1992) and can involve supplementary feeding of weaners to improve both their growth and survival rates (Winks *et al.*, 1972). Further, the seasonal variation in tropical environments can be much greater than in temperate environments and this suggests that data and models developed in temperate environments are not suitable for tropical environments.

Fertility

The variability between seasons is significant for both temperate and tropical environments. Bolton *et al.* (1987b) and McCarter *et al.* (1991b) have shown highly significant differences in fertility between seasons in temperate environments. There is also a large body of evidence showing season to be a significant factor affecting fertility in tropical environments (Plasse *et al.*, 1968; Rudder and McCamley, 1972; Richardson *et al.*, 1975, see reviews by Galina and Arthur, 1989 a,b).

Whereas in temperate environments spring calving has been shown to be more productive than fall (autumn) calving (McCarter *et al.*, 1991b), in tropical environments the wet season has been shown to be more productive than the dry season. Studies by Rudder and McCamley (1972) in northern Australia (latitude 23°S) and Wilson (1985) in Mali (latitude 13°N) have shown a significantly positive relationship between the peak in the calving season and the wet season of about 10 months earlier. However, Domínguez *et al.* (1993) reported that high summer rainfall in the subhumid tropics of Mexico (latitude 21°N) has an adverse effect on the fertility of Brown Swiss cows. The effect of rainfall on fertility is not clear-cut, since other factors, such as timing of rainfall, humidity and genotype, may also be important variables.

1.3.3 Maternal environment

Growth and Fertility

Adverse effects in certain years and seasons on the growth performance of calves and the reproductive performance of cows are moderated by the cow's maternal environment. The shielding from the stresses of climate and parasites is initially provided in the uterus and then, following birth, the calf is assisted with survival and growth by the mothering ability and milk production of the dam. It has long been established (see BIF, 1981; NBRS Recording Manual, 1982) that to accurately assess the growth performance of calves, the calf weights and weigh gains have to be adjusted or corrected for maternal effects. The degree to which post-partum assistance is provided by the dam primarily depends upon the level of her current milk production (Jeffery *et al.*, 1971; Rutledge *et al.*, 1971; Koch, 1972). However, the difficulty in obtaining estimates of milk production in beef cows, especially under a rangeland production system, normally precludes using milk production as a fixed effect to describe the growth performance of calves. The fixed effects most often used to describe maternal environment are the age of the dam and her lactational status the previous year. As with calf growth rates, an accurate assessment of a cow's reproductive performance can also require consideration of both the cow's age and previous lactational status. Thus, maternal effects are critical components of models of genetic evaluation.

1.3.4 Age of cow

Growth

In temperate environments most published reports support the view that age of dam is a significant fixed effect for the calf growth parameters of birth weight, weight gain between birth and weaning and weaning weight. In general, as the age of the dam increased form 2 to 4 years so did all three growth parameters. The optimum maternal environment, as measured by calf weaning weights, was achieved by cows from 5 to 10 years of age (Cundiff *et al.*, 1966; Martojo *et al.*, 1972; Lubritz *et al.*, 1989). After a cow has reached 10 years of age there can be a significant reduction in weights of their calves (Srinivasan and Martin, 1970; Bair *et al.*, 1972; Martojo *et al.*, 1972).

In temperate environments the variation in age of dam correction factors is so negligible that a standard set of factors is applied to all weaning weights. The U.S. Beef Cattle Records committee recommend multiplicative correction factors of 1.15, 1.10, 1.05 and 1.00 be applied to 205-day weaning weights of calves reared by 2, 3, 4, and 5-9 year old dams (Cardellino and Frahm, 1970). In an experiment comparing these correction factors with corresponding factors derived from 205-day weaning records of 404 Herefords and 822 Angus under the range conditions of Oklahoma (latitude 35°N), Cardellino and Frahm (1970) found a close agreement between the two sets of factors although there was a small loss of accuracy for Herefords. The U.S. correction factors were initially adopted in Australia by AGBU for 2, 3, 4 and 5+ year old dams for a weaning weight at 200 days, and used in both southern and northern environments (NBRS Recording manual, 1981). More recently, the age-of-dam effect has been modified by increasing the age-class levels. The ages of dam at 2, 2.5, 3, 4, 5, 6, 8, 10 and 12+ years have been adjusted to a standard age of 5 years by a quadratic adjustment for weights of calf at birth and ages at 200, 400 and 600 days (BREEDPLAN Handbook, 1991).

As in temperate environments, a majority of the reports on factors affecting calf growth rates in tropical environments nominate age-of-dam as a highly significant fixed effect. In tropical environments, cows 5 years of age and older rear calves significantly heavier than 4 year olds which in turn rear calves significantly heavier than 3 year old cows (Rudder *et al.*, 1982a; Burrow *et al.*, 1991; Fordyce *et al.*, 1993a). In less stressful tropical environments calves from 3 year old cows are heavier than calves from 2 year old heifers (Lapworth *et al.*, 1976). However, studies of maternal effects, from regions of relatively high environment stress, report that females do not enter the breeding herd until they are 2 years of age and first calve as 3 year olds, whereas, in the more benign environments 3 year old cows were lactating during the previous breeding season.

The variation in the effect of age of dam in highly stressful tropical environments can be very pronounced. In the dry tropics of central Queensland (latitude 23°S), Burrow *et al.* (1991) found that progeny from dams aged 5 years or more were consistently 3-4% heavier than progeny from 4 year old dams. For West African Shorthorn crossbreds in the tropical environment of Ghana (latitude 8° N) the progeny from 7 year old cows were heaviest and 9 and 15% heavier than progeny from either 5 or 4 year old cows respectively (Ahunu *et al.*, 1993). Thus, the variation in environmental stress between the different regions of the tropics is such that age of dam correction factors may only be applicable to that region's production system, environment and genotype, and not transferable to other regions.

Fertility

In temperate environments, the early research work on factors affecting female fertility were concerned with the effects of age-of-cow on reproductive rates, but, as production systems shifted to calving heifers as 2 year olds, rather than 3 year olds, researchers began to concentrate on age at puberty and dystocia of heifers (Wiltbank *et al.*, 1961). The early work showed that 2 to 3 year old heifers had a lower fertility than 4 to 10 year old cows and a significant drop in pregnancy rate occurred once the cows had reached 10 years old. More recently the research effort has been directed at lowering the age at puberty (Newman and Deland, 1991; Martin *et al.*, 1992) and the elimination of dystocia, especially in heifers, as this age group is more prone to calving difficulties than older age groups (Laster *et al.*, 1973b; Whythes *et al.*, 1976; Cubas *et al.*, 1991; Newman and Deland, 1991; Turner and Farnsworth, 1993).

In tropical regions also, the age of the cow has a significant effect on fertility but here the variation in intercalving interval and reproductive rate between the different age groups can be extreme. In general, in tropical environments, the reproductive rate of heifers calving first as 3 year olds is relatively high, the first calving interval is longest, the intercalving intervals over the next 3 or 4 calvings are shortest and as the animal ages (over 8 years old), the intercalving interval again increases (Koger *et al.*, 1962; Buck *et al.*, 1976; Mackinnon *et al.*, 1989; Ray *et al.*, 1989; O'Rourke *et al.*, 1991a,b). In their study of 2299 pregnancy records of Brahman cross and Sahiwal cross females in northern Australia (latitude 20°S) Holroyd *et al.* (1990b) reported the following range in pregnancy rates between cow age groups and years; maidens 29% and 86%; first calf lactating cows 8% and 71% and mature lactating cows, 15% and 91%. Thus, the age of a cow can have a significant bearing on her calving rate but unlike temperate regions in the tropics, the variation between the different ages of dam can be extreme.

1.3.5 Previous lactational status

Growth

In temperate regions, reproductive rate is so high that the small number of cows that remains non-pregnant at the end of the breeding season is usually culled, this being a standard recommendation for the industry (e.g. BIF, 1981; NBRS Recording Manual, 1982). However, if the non-pregnant cows are not culled but retained in the breeding herd, the effects of their non-lactational status on the productivity of their next parity are usually not considered. Of the relatively few reports that have been concerned with the effects of the previous lactation status (see Maurer and Echternkamp, 1985, for references) most have found the effects on calf growth rates to be non-significant (e.g. Notter *et al.*, 1978).

The lower reproductive rates of cows in tropical environments means that some or all non-pregnant cows are retained and enter the breeding season as non-lactating cows. However, numerous reports in the literature of statistical models that describe calf growth rates (both pre- and post-weaning) either ignore the effects of the previous lactation status (Creek and Nestel, 1964; Deese and Koger, 1965; Iboeje, 1986; Mwandotto *et al.*, 1988; Fordyce *et al.*, 1993a,b; Tawah *et al.*, 1993) or the authors do not fit this effect as the dataset lacks information on the previous lactation (Robinson, 1990; Robinson and O'Rourke, 1992). Burrow *et al.* (1991), found for a single "Belmont" calf crop of Brahman, Hereford-Shorthorn (HS), Brahman x HS (BX) and Africander x HS (AX) calves, that the previous lactational status had no effect on calf weights or daily gains when weights of calves were adjusted for the age of the calf. At the same location, using age-adjusted weights of a single calf crop of similar genotypes to those used in the Burrow *et al.* (1991) study, but in a different year, Frisch and Vercoe (1984) found that the effect of the previous lactation was a significant component in the model. Other workers, at "Belmont" and elsewhere in tropical and sub-tropical locations, using larger number of years in their datasets, also found this effect to be significant (Berruecos and Robinson, 1968; Barlow and O'Neill, 1978,1980; Thorpe *et al.*, 1981; Hetzel *et al.*, 1990). In these studies calves whose dams were non-lactating the previous year were heavier at both birth and weaning, than calves whose dams were lactating the previous year. Thus, in the analysis of calf growth rates in temperate environments, the effects of previous lactational status are minor and can often be ignored, but in tropical environments, the adjustment for both maternal effects can be an essential consideration, not only for growth rates to weaning, but also post-weaning growth rates to 18 months of age (Mackinnon *et al.*, 1991).

Fertility

In relatively stressful environments, whether a cow goes into the breeding season with a calf at foot can also be determined by her lactational status at the previous breeding season. The effects of the previous lactational status are generally seen as being more important than the age of the cow. Compared to non-lactating cows, the calving rate of lactating cows is reduced by an average of 20% (Preston and Willis, 1974). The importance of lactational anoestrus in the sub-tropics of Florida (latitude 20°N) is indicated by a quote from Koger *et al.* (1962, p. 17) "age of cow exerted an effect on reproductive performance second in magnitude only to lactational status". Other studies from Florida and other locations in the tropics confirm the significance of the effect of previous lactation on pregnancy status or weaning rate (Buck *et al.*, 1976; Franke, 1980; Holroyd, 1985; Frisch *et al.*, 1987; Mackinnon *et al.*, 1989; Voh and Otchere, 1989; O'Rourke *et al.*, 1991a; Davis *et al.*, 1993).

1.3.6 Sex of calf

Growth

The effect of sex on growth of calves is well documented and is an important consideration for genetic evaluation models. It is generally accepted that in both temperate and tropical environments, male calves are born later (Jeffery *et al.*, 1971; Franke *et al.*, 1973; Preston and Willis, 1974; Barlow and O'Neill, 1978) heavier (Bair *et al.*, 1972; Barlow and O'Neill, 1978; Pell and Thayne, 1978; Burrow *et al.*, 1991; Ahunu *et al.*, 1993) and growth at a faster rate than females (Jeffery *et al.*, 1971; Barlow and O'Neill, 1978; Winroth, 1990; Burrow *et al.*, 1991; Fordyce *et al.*, 1993a).

Fertility

In general, the effect of sex of calf on the fertility of their dams is considered of no consequence. The few studies that have tested for the effect have found it to be non-significant (Warnick *et al.*, 1967; Aaron and Thrift, 1990, Aaron *et al.*, 1990).

1.3.7 Genotype

Growth and Fertility

A major contributing factor to the different levels of productivity in the various geographical regions is the genotype used in those regions. *Bos taurus* breeds evolved in temperate regions and are utilised in Europe and the temperate environments of North America and Oceania. The *Bos indicus* derived breeds, although occasionally used in the benign temperate regions, predominate in the tropics, the region in which they evolved.

The level of productivity attained in a region has been shown to be dependent upon a combination of genetic potential for production and resistance to environmental stress (Frisch and Vercoe, 1982). In temperate environments, where environmental stresses are relatively low, productivity depends mainly on genetic potential for growth (e.g. metabolic rate), and fertility (e.g. age at puberty). *Bos taurus* are more productive than *Bos indicus* in these environments because of their higher production potential. Conversely, the realisable productivity in the more environmentally stressful tropics depends, not only upon the production potential of the genotype, but also the genotype's resistance to the environmental stresses of the region (e.g. high ambient temperatures). Hence *Bos indicus* breeds, because of their relatively high levels of resistance to the environmental stress of the tropics, are more productive than *Bos taurus* breeds in these environments.

1.4 Interactions

Models of growth and fertility are complicated by interactions that can arise between these fixed effects. In the tropics such interactions are important because the different levels of the fixed effect differ in their sensitivity to the variations in the environment.

1.4.1 Interaction between the maternal and physical environments

Growth

In the limited number of studies that have specifically looked at the interaction between maternal effect and environments for growth rate of calves, the interaction was found to be significant. Important differences were found in different environments when either age of dam or previous lactational status was considered (Koger *et al.*, 1962; Harwin *et al.*, 1966; Seebeck, 1973; Bailey and Koh, 1974; Pell and Thayne, 1978; Seifert *et al.*, 1980; Frisch *et al.*, 1987; Itulya *et al.*, 1987). How quickly younger cow achieved maximum production, and at what age older cows were able to maintain maximum levels of production, generally depend upon the environment under which the cows were grazed. In experiments where good and poor nutritional environments were used (e.g. Bailey and Koh, 1974) or years were categorised as either good or poor (e.g. Itulya *et al.*, 1987), both younger and older cows were relatively more disadvantaged in the poor environments, or poor years. Presumably, reasons for this are that younger cows are more handicapped in the less optimal environment, because they require energy for their own growth as well as lactation, while aged cows are more susceptible to the ageing process.

1.4.2 Interaction between genotype and the physical environment

Time of calving

The time of calving of cows in tropical environments is related to genotype. A number of studies have found that the calf date of birth was later for Brahman-sired calves than for calves sired by *Bos taurus* bulls (Reynolds *et al.*, 1979; Williams *et al.*, 1990). Similarly, cows of lower Brahman content have been shown to have earlier calving dates than cows of higher Brahman content (Madalena and Hinojosa, 1967; Holroyd *et al.*, 1990a). The differences in time of calving has been attributed to high grade Brahmans conceiving later in the breeding season and having a longer gestation period compared to cows of low Brahman content (see Preston and Willis, 1974 and Galina and Arthur, 1989b,c).

Growth and Fertility

The interaction between genotype and environment has been reported extensively for both growth and fertility (Barlow and O'Neill, 1978;

Setshwaelo, 1990; McCarter *et al.*, 1991c; Brown *et al.*, 1993a,b; Morris *et al.*, 1993; Chenoweth, 1994). In a study by Bolton *et al.* (1987a) at Oklahoma (latitude 35°N), three genotypes of dams were used (0, ¼ and ½ Brahman content) and the interaction between the proportion of Brahman and season of birth was found to be significant for weaning weight but not for birth weight. The interaction arose because it was mainly in the spring-born calves that the preweaning daily weight gain and weaning weight increased as the proportion of Brahman increased. Spring-born calves were raised in summer (minimum and maximum temperature of 17 to 36°C) while autumn-born calves were raised in the winter (minimum and maximum temperatures of -6 to 13°C) and thus it appears that the heterotic advantage from the *Bos indicus* seen in the warmer environment, was not realised in winter because of this genotype's poor adaptation to cold environments.

The interaction between genotype and environment also provides an explanation of heterosis for growth and fertility in tropical environments. When compared to *Bos indicus* breeds, the *Bos taurus* breeds possess inherently high genetic potential for both growth, as measured by feed intake and fasting metabolism (Frisch and Vercoe, 1977,1982), and fertility, as measured by calf crop, (Frisch *et al.*, 1987). On the other hand, *Bos indicus* breeds, represented by Brahman (Indian *Bos indicus*), possess high genetic potential for both heat and parasite resistance (Frisch and Vercoe, 1984), and their low maintenance requirement (Frisch and Vercoe, 1982) acts as a survival mechanism during times of limited nutrition (Frisch, 1972,1973). The combination of the qualities of the two genotypes explains the heterosis that is observed in the F_1 *Bos indicus* x *Bos taurus* in a stressful tropical environment (Frisch, 1987,1992).

The interaction between genotype and environment has implications for the within-breed genetic evaluation as the interaction adds to the complexity of estimating genetic change. As suggested by King and Smith (1984), if the interaction is appreciable the evaluation may need to be undertaken in a variety of environments.

1.4.3 Interaction between genotype and maternal environment

Growth

A large body of evidence indicates that researchers undertaking genetic evaluation of growth should consider the interaction between genotype and maternal environment in their models. Franke and Oviedo (1992) note that age of dam adjustments have been studied much more extensively in purebreds than in crossbreds. These authors also note that variation in the adjustments involving crossbreds was primarily due to the proportion of Brahman in the dam. Other studies have indicated that the effects of age of dam on birth and weaning weight are less in Brahman and/or Brahman crossbred dams than in British dams (Seifert, 1975; Brown *et al.*, 1993a, b). In a study of Brangus cattle, Cravey and Turner (1990), found that the effects of age of dam on lactating females closely paralleled results for Brahman rather than the British breeds. The Brangus females produced better calves at younger ages and have an increased longevity when compared to females of British breeds.

1.4.4 Interaction between genotypes, sex of calf and environment

Growth

Itulya *et al.* (1987) argue that not only should the age of dam correction factors be specific for the environment under which the dams nurse their calves but also for sex of calf. Their study of the growth rates of Hereford calves on rangeland at Arizona, along with numerous other reports (e.g. Pahnish *et al.*, 1964; Cundiff *et al.*, 1966; Harwin *et al.*, 1966) have shown that males are more affected than females in poor versus good environments. Itulya *et al.* (1987) have found that the range in age of dam correction factors for weaning weight of males was 12.3 kg during the good years and 21.9 kg during the poor years. Comparable values for heifer calves were 6.5 and 10.8 kg respectively. Young and old dams provide a less optimal maternal environment than dams between 5 and 10 years of age. As males have been shown to be more sensitive than females to an unfavourable environment, males are more adversely affected by the less favourable maternal environment of young and older dams (Harwin *et al.*, 1966; Bovard and Weinland, 1973; Burrow *et al.*, 1991; Fordyce *et al.*, 1993a; Brown *et al.*, 1993a,b). It also follows, males of the genotype that is less resistant to environmental stress, will be more affected than males of the more resistant genotype (Seifert *et al.*, 1974; Frisch, 1981; Franke and Oviedo, 1992).

Pahnish *et al.* (1964) contend that males may be more sensitive to alterations in the environment because they are larger than females and need more nutrients to fully express their growth potential. However, the male sex hormone testosterone, or conversely the female sex hormone oestrogen, may play an important role in the interaction between environment and sex (Frisch and Hunter, 1990a,b). This is because females have been shown to be more resistant than males to the ecto- and endo- parasites of the tropics (see Frisch, 1981). The significance of the relationship between nutrition, parasite resistance and sex hormone has yet to be fully investigated. Nevertheless, for regions that are characterised by relatively high environmental stress both age of dam and sex of calf correction factors should be specific, not only for the genotype, but also for the region.

1.5 Covariates

Covariates (independent variables) are incorporated into models so that those variables that describe a cause-and-effect relationship with the dependent variables can be identified.

1.5.1 Calf day of birth

Growth

Beef systems that employ a restricted breeding and calving season endeavour to manage the peak in the number of calvings to coincide with the optimum nutritional environment of the region. As pointed out by Elings *et al.* (1971), a substantial spread of the calving period will necessarily include periods when the environmental conditions are less than optimal. Hence, adjusting calf growth rates for time of birth has long been considered an important correction in the analysis of the growth performance of calves (Nelms and Bogart, 1956).

Not all researchers who have investigated the factors affecting growth rates of calves consider time of birth in their statistical models as either a main effect or covariate (e.g. Vesely and Robinson, 1972; Francois *et al.*, 1973; Notter *et al.*, 1978; Brown *et al.*, 1993a,b). Presumably, these researchers regarded time of birth to be unaffected by environmental conditions.

However, the great majority of studies do consider time of birth in models of calf growth performance. Of these studies, a small number have found time of birth to be significant for birth weight but non-significant for weaning weight (Seifert, 1975). In other studies, time of birth was significant for both birth weight and weaning weight but differences were not apparent by 8 months of age (Neville, 1962) or by 553 days of age (Rudder *et al.*, 1975). Fordyce *et al.* (1993b) and Lapworth *et al.* (1976) found time of birth to still be significant at 730 days and 890 days respectively. There is considerable variation in the effects of the calving season in these studies.

In general, time of birth was found to be a significant component in the growth rates of calves. This was regardless of whether season of birth (Iloeje, 1986; Taylor *et al.*, 1991; Tawah *et al.*, 1993), month of birth (Cundiff *et al.*, 1966; Gomez *et al.*, 1972; Mwandotto *et al.*, 1988), or day of birth (Rudder *et al.*, 1975; Barlow and O'Neill, 1978; Frisch and Vercoe, 1984; Hetzel *et al.*, 1990; Robinson, 1990) was used as the variable to describe time of calving. Furthermore, the effect of time of calving on growth rate of calves was not consistent with some studies showing early born calves to be advantaged over late born claves, (Lesmeister *et al.*, 1973; Seifert *et al.*, 1974; Keller and Brinks, 1978) while in other studies the converse was true (Jeffrey *et al.*, 1971; Neville *et al.*, 1974; Rudder *et al.*, 1975; Newman and Deland, 1991; Fordyce *et al.*, 1993a,b). These studies suggest that in the analysis of any dataset, from either temperate or tropical regions, time of birth must be included in the models used to describe growth.

1.5.2 Time of calving for heifers

Fertility

Cows that calve late in the calving season generally have lower reproductive rates and produce less kilograms of calf than cows that calve early in the season. However, this relationship is not always consistent and this inconsistency is usually linked to the different environments. Reviews by Galina and Arthur (1989a), Martin *et al.* (1992), Patterson *et al.* (1992) and Schillo *et al.* (1992) indicate that there is an array of environmental and genetic variables interacting with heifer reproductive physiology and subsequent time of calving of those heifers.

In the production systems in temperate environments, one of the aims of the majority of cattle management strategies is for replacements heifers to conceive at 14 to 16 months of age and calve at 2 years of age. In order for heifers to conceive at this age they should undergo two or three oestrous cycles prior to the commencement of the breeding season, as the conception rate from the first oestrous is lower than from subsequent oestrous cycles (Byerley *et al.*, 1987). Ideally replacements heifers need to have attained puberty by 12 months of age, but, a high variation in the onset of puberty in heifers produces a correspondingly high variation in the time of calving. Numerous studies have demonstrated that a heifer calving late in the calving season would continue to calve late in subsequent seasons (Burris and Priode, 1958; Smith *et al.*, 1989; Osoro and Wright, 1992), and be associated with lower reproductive rates and/or lower calf weaning weights (Roberts *et al.*, 1970; Lesmeister *et al.*, 1973; Olsen *et al.*, 1993).

Unlike in temperate regions, in tropical regions where the level of stress is such that heifers are managed to calve first as 3 year olds, the issue of age at puberty in heifers is of less importance because the majority of heifers have usually attained puberty before the start of the breeding season (D'Occhio *et al.*, 1992). In temperate regions, heifers calving first as 2 year olds tend to calve in the middle of the calving season (Nelms and Bogard, 1956), whereas in the tropics, heifers calving as 3 year olds calve early in the calving season (Frisch, 1973; Davis *et al.*, 1993). Thus, there is very little resemblance between the time of calving for heifers in temperate versus tropical environments and datasets for the genetic evaluation of heifer fertility would be incompatible between the two environments.

1.5.3 Time of calving for cows

Fertility

In production systems in which a fixed breeding season is employed, a critical issue for the productivity of lactating cows is the cow's ability to rebreed. The relationship between resumption of oestrus and time of calving is not consistent and a major influence on this relationship is the environment. In temperate environments, the majority of studies have found that later calving cows have shorter postpartum intervals (Morris, 1980; Montgomery *et al.*, 1980; Osoro and Wright, 1992). Montgomery *et al.*, (1985), using Angus cows in New Zealand (latitude 45°S), found that even when cows were fed a constant high level of nutrition, the postpartum anoestrus interval was longer in early calving cows (67 days) than in late calving cows (57 days). Olsen *et al.* (1993) obtained similar results for Angus and Beefmaster cows at Utah (latitude 40°N). On the other hand, in tropical environments, numerous studies have found that late calving cows have lower reproductive rates than early calving cows (Buck *et al.*, 1976; Holroyd, 1985; Rudder *et al.*, 1985; Frisch *et al.*, 1987; O'Rourke *et al.*, 1991a,b,1992). Clearly the factors affecting the time of calving are different in cows in the two environments.

Unlike in temperate regions, in tropical and semi-arid regions a substantial proportion of the breeding animals consist of non-lactating cows. These non-lactating cows contribute significantly to the early calving rate of the herd. In their 5 year study of female reproductive rates in northern

Australia (latitude 13°S), O'Rourke *et al.*, (1991a) found that non-lactating cows had very high conception rates (93 to 97%) with 89% of conceptions occurring during the first two months of the calving season. Neville *et al.* (1987) showed that non-lactating cows calved, on average 17 days before lactating cows, while in the study by Hetzel *et al.* (1989) and Ray *et al.* (1989) the average difference was 19 and 11 days, respectively. As with time of calving for heifers, the time of calving for cows is vastly different between temperate and tropical environments.

1.5.4 Indices for fertility

Production systems in tropical environments, unlike those in temperate environments, are characterised by pastures that are subjected to distinct wet and dry seasons. During the wet season, pasture resembles that in a temperate environment and is actively growing, nutritious and highly palatable and the cattle gain in weight. However, during the dry season both the nutritive value and digestibility of the pasture deteriorate and cattle may become undernourished and may lose weight (Hunter and Buck, 1992). The extensive periods of undernutrition will have a detrimental effect of puberty in heifers and both the milk production and resumption of oestrus in lactating cows (see reviews by Lammond, 1970; Topps, 1977; Entwistle, 1983; Galina and Arthur, 1989a,b,c). As in temperate environments, in tropical environments the cow's liveweight, change in weight and condition scores are useful indices of the relationship between undernutrition and fertility (Richardson *et al.*, 1975; Buck *et al.*, 1976; Couchman, 1983; Rudder *et. al.*, 1985; Frisch *et al.*, 1987; Mackinnon *et al.*, 1989; Fordyce *et al.*, 1990; Holroyd *et al.*, 1990a; MacGregor and Swanepoel, 1992).

The seasonality of pastures in the tropics and subtropics can also result in malnutrition of cattle, where malnutrition is defined as the intake of an inadequate diet. In these environments, problems with undernutrition (low intake of energy and protein) are exacerbated by the pasture being deficient in minerals (e.g. phosphorus, sodium and sulphur), trace elements (e.g. copper and cobalt) and vitamins (e.g. ß-carotene, which is the animals natural source of Vitamin A). The influence of minerals and vitamins on fertility of cattle has been well reviewed and discussed by Hurley and Doane (1989), Swanson (1989) and Hunter and Buck (1992). Thus, in the tropics, critical limits of minerals and vitamins can be a significant contribution to the environmental variation in fertility.

1.5.5 Indices for heifer fertility

Just as there is a minimum age at which heifers attain puberty there is also a minimum body weight and prepubertal gain in weight. A heifer's body weight has long been considered a major factor affecting age at puberty (see review by Joubert, 1963), and is considered more important than age (Arije and Wiltbank, 1971). Age at puberty has also been shown to be influenced by prepubertal gain in weight (Arije and Wiltbank, 1971; Short and Bellows, 1971; Laster *et al.*, 1972).

In regions where environmental stress is relatively high, low post-weaning growth rates dictate that the target weights desired for the production system are not met until the heifers are 2 years of age (Lammond, 1970; Goddard *et al.*, 1980; Entwistle, 1983; MacGregor and Swanepoel, 1992). In northern Australia (latitude 20°S), an estimated target mating weight for *Bos indicus* heifers of 24 to 27 months of age is usually between 280 and 320 kg to achieve an 85% pregnancy rate (Holroyd, 1985). However, because the relationship between a heifer's liveweight and fertility is complicated by interactions between genotype, age, change in body weight, body condition (fat reserves), and the quantity and quality of available nutrition, it is very difficult to make accurate recommendations for a target weight for heifers in stressful environments.

Bronson and Rissman (1986) note that little is known about partitioning of nutrients between reproductive and non-reproductive requirements for heifers. If heifers are overfed (and over fat) because of an overabundance of pasture and/or the overuse of supplementary feeding, there is a detrimental effect on puberty, reduced conception rates at first breeding, high embryonic mortality and a decreased mammary gland development with a consequence of lower milk production (see Patterson *et al.*, 1992 for review). Hence, Greer *et al.* (1983) and Patterson *et al.* (1992) both concluded that age at puberty is not determined by weight per se, but rather by an undetermined array of physiological conditions that also result in a given body weight for normal growth.

1.5.6 Indices for cow fertility

Whether or not a lactating cow resumes oestrous activity after calving depends upon both the quality and availability of feed. Resumption of oestrus also depends upon the female's genetic capacity to partition her dietary intake between the conflicting demands for reproduction and lactation. A special case is the dietary intake of a young cow with her first or second calf at foot. The dietary intake of this female must not only meet demands for her continued growth and resumption of oestrus but also her lactation. If the available nutrients are partitioned towards meeting the demands of lactation, and away from reproductive functions, the return to oestrus is delayed. In these females, the interrelationship between nutrition, lactation and the duration of postpartum anoestrus, has been shown to be principally associated with the intake of energy rather than the intake of protein (see reviews by Hanzen, 1986; Butler and Smith, 1989; Randel, 1990; Hansen, 1991).

Although the dairy and beef production systems have little in common, lactational anoestrus can occur in cows from both systems. Hence, the relationship between the cows energy status and her resumption of ovarian activity is common to both dairy and beef cows. The most important stage of lactation is the period from calving to peak lactation, which generally occurs at between 3 and 6 weeks after calving (Cobbey and Le Du, 1978). During this stage of lactation the demand for energy is highest. A dairy cow producing 35kg of milk daily, requires three times more energy for milk production than for body maintenance (Butler and Smith, 1989). If her total demand for energy cannot be met by dietary intake, then there must be a mobilisation of her bodily reserves of energy. The resultant negative energy balance and the rate of mobilisation of body reserves, appear to directly affect the postpartum interval and to lower conception rate (Butler and Smith, 1989; Hansen, 1991).

In other studies where the environmental stress was low, there was not always a relationship between postpartum energy balance and ovarian activity (Stricker *et al.*, 1979; Carroll *et al.*, 1990; Harrison *et al.*, 1990) suggesting that other factors can obscure or override effects of energy balance. These other factors could be the intake of vitamins and minerals, some of which are known to influence reproduction in the cow (Hurley and Doane, 1989; Swanson, 1989).

The adverse effect of undernutrition on the fertility of lactating cows is more pronounced in herds in tropical and sub-tropical regions than in herds in temperate regions. In northern Australia, the effects of lactation are such that lactating cows have lower pregnancy rates than non-lactating cows (e.g. Frisch *et al.*, 1987; Anderson *et al.*, 1988; Mackinnon *et al.*, 1989; O'Rourke *et al.*, 1991a,b), whereas in southern Australia and other temperate environments, where undernutrition is rarely a problem, lactating cows can have higher pregnancy rates than non-lactating cows (Young 1968; Reynolds *et al.*, 1979,1986). Numerous studies in relatively stressful environments such as northern Australia, conclude that the anoestrous period in lactating cows is primarily a reflection of the interaction between nutrition and lactational status (see reviews by Entwistle, 1983; Galina and Arthur, 1989b,c). Presumably the suckling stimulus (Wettemann *et al.*, 1978; Williams *et al.*, 1982) and maternal bonding (MacMillan, 1983; Eduvie and Dawuda, 1986) are common to lactating cows of both low and high stress environments, and the difference between the two environments is the extra nutritional demands of lactation on body reserves where the dietary intake is reduced.

For lactating cows in temperate and in tropical environments, their liveweight, their change in weight during the breeding season and their condition score are useful indices of their capacity to rebreed whilst lactating (see review by Randel, 1990). In general, when liveweight, weight gain and condition score are increased, the reproductive rates of lactating cows are also increased (Richardson *et al.*, 1976; Buck *et al.*, 1976; Goddard *et al.*, 1980; Richards *et al.*, 1986; Frisch *et al.*, 1987; Entwistle, 1989; Mackinnon *et al.*, 1989; MacGregor and Swanepeol, 1992).

Although the postpartum change in body weight and condition score have been shown to be related to postpartum anoestrus, work by Richardson *et al.* (1975) and Steenkamp *et al.* (1975) have shown that the best indicator of a cow's ability to rebreed is her liveweight at the start of the breeding season. Cows whose liveweight is well above their target weight are able to lose a substantial degree of weight and condition and yet still rebreed successfully. On the other hand, very thin cows would still not reach their target for rebreeding even if they were to gain a small degree of body weight and condition during the postpartum period. Entwistle (1983) places the three indices in context by noting that both liveweight and condition score are indicators of a cow's long-term nutritional status whereas the change in body weight during the postpartum period is a reflection of her short-term nutritional status. Hence, in tropical environments, all three indices should be considered in models of genetic evaluation of fertility.

In spite of both interactions and covariates being extensively reported in the literature, the methodology by which these components are incorporated into a national genetic evaluation program has yet to be developed. Notter (1991) makes the point that the accommodation of the interactions between genotype and environment has been made difficult because of the lack of unambiguous definitions of both genotype and environmental factors. Indeed, clearly defined definitions of all factors affecting growth and fertility will be required before interactions and covariates can be quantified for genetic evaluation models that are suitable for a tropical environment.

1.6 Aims of study

A large number of studies have identified the major factors that effect productivity of beef cattle in both temperate and tropical environments. Only some of the factors identified in temperate environments are important in tropical environments whereas , a number of factors are unique to the tropics. Genetic prediction models that are to be used in tropical environments should only incorporate factors that are pertinent to tropical environments. Few studies have analysed the components of models of both growth and fertility (i.e. management groups, fixed effects, interactions and covariates) for both *Bos taurus* and *Bos indicus* cattle in a tropical environment. High variability between years is synonymous with dry tropical environments yet few published studies have categorised this variability into good and poor environmental conditions.

The present study aimed to identify the significant non-genetic components of variation of the growth of calves and the pregnancy rates of heifers and cows from both *Bos taurus* and *Bos indicus* genotypes in a dry tropical environment. The study investigated appropriate dependent variables, fixed effects, interactions and covariates that could be used to describe models of growth and fertility in this environment. The contribution of additive genetic variation (random effects) was not considered as this was beyond the scope of this study where the primary aim was to estimate the importance of the various non-genetic components that describe growth and fertility. The non-inclusion of additive genetic effects was unlikely to have greatly biased the major conclusions of this study because of the large random sample of sires used in the study. Further, only a single management group was used in this study as data from other management groups was incomplete. As observed by Itulya *et al.* (1987) and Baker *et al.* (1991) the influence of different management groups (or production systems) on genetic parameters and therefore genetic improvement programs remains to be evaluated. Hence, animals that had been treated differently from the general herd (e.g. mating heifers as yearlings, control of parasties) were removed from the datasets so as to avoid the need to consider different management groups in the analysis. The study will, however, investigate the sensitivity of the different genotypes and fixed effects to changes in environmental conditions. The value of the significant components of variation and their sensitivity to changes in environmental conditions is discussed in relation to appropriate models of genetic evaluation that can be used in the genetic improvement of on-farm productivity in northern Australia.

CHAPTER 2

MATERIALS AND METHODS

2.1 The production environment and genotypes

2.1.1 Environmental conditions

The data were collected from 1974 to 1990 at the CSIRO National Cattle Breeding Station, "Belmont", which is a 3650 ha property located 26 km north of Rockhampton, Queensland, Australia (latitude 23° S, longitude 150° E).

Both native and improved pasture species grow on "Belmont". About one third of the property is subject to flooding by the Fitzroy River and this area is grassed with native grass species such as common couch (*Cynodon dactylon*), water couch (*Paspalum distichum*) and improved pasture species including the grasses, green panic (*Panicum maximum var. trichoglume*) and buffel (*Cenchrus ciliaris*) and the legume, seca stylo (*Stylosanthes scabra*). Improved pastures have been fertilised with superphosphate to maintain the soil P level between 15 and 20 ppm.

The climate is dry tropical with a summer wet season of variable duration and low reliability. The variation in rainfall between years can be as great as the rainfall variation within a year. The rainfall for 1982 (343 mm) was well below the average for "Belmont" (820 mm) and the property was in drought during the summer of 1982/83 (118 mm) (Anon, 1983). This extended period of low rainfall was followed in 1983 by a flood in March and an autumn rainfall of 696 mm. The mean daily minimum and maximum temperatures for summer and winter are 22°C and 32°C (January) and 11°C and 23°C (July) respectively (Anon, 1976). The mean daily relative humidity is in the range of 63 to 69% (Anon, 1976).

The effects of climate variability on the productivity of cattle on "Belmont" are accentuated by periodic infestations of internal and external parasites, disease and noxious shrubs. The main parasites are cattle ticks, (*Boophilus microplus*), buffalo flies, (*Haematobia irratins exigua*) and gastrointestinal helminth species, (*Haemonchus, Oesophagostomum* and *Cooperia*) (Frisch and Vercoe, 1984; Bean *et al.*, 1987; Mackinnon *et al.*, 1991). Both the bacterial eye disease, Bovine Infectious Kerotoconjunctivitis (BIK) (Frisch, 1975) and the viral disease Bovine Ephemeral Fever, periodically cause loss in productivity. Ingestion of the noxious shrub, *Lantana camara* can also cause loss of productivity and/or death (Frisch *et al.*, 1984).

2.1.2 The genotypes

In the early 1950's, CSIRO established various beef cattle genotypes on "Belmont" to study the performance of these genotypes in a tropical environment. At that time Herefords and Shorthorns were purchased from industry herds, crossed and then interbred to produce the HS, a line representing the *Bos taurus*. In 1966, a selected line, the HSS, was established from bulls selected for high post-weaning weight gain to 24 months. Approximately half of the line remained a randomly selected control line (HSR). The HSS was not closed until the late 1970's when breeding animals ceased to be transfered from the HSR. The number of cows of breeding age in the HSS line averaged about 120 animals per year.

In 1953 four Brahman bulls were imported from the USA and crossed with Hereford and Shorthorn cows. The Brahman x Hereford and Brahman x Shorthorn were crossed reciprocally to form the Brahman cross (BX) line. After 1959 the BX line was closed and interbred. Between 1974 and 1990 cow numbers were maintained at about 160 animals per year.

The imported Brahman bulls were also used to provide the foundation of the "Belmont" Brahman line, a line representing the *Bos indicus*. Prior to

1970 the Brahman line was kept at 24 breeding cows and managed separately from the general herd. During the 1970's the Brahmans were maintained at about 45 breeders and the line was closed apart from the use of 2 industry purebred bulls and inclusion of backcross calves born to F_1 Brahman x *Bos taurus* cows. The process of including ½ breed cows to produce 3/4 backcross progeny continued until 1974. From 1980 onwards the breeder numbers were increased in the following years with the purchase from several commercial and stud herds of registered and unregistered cows of both high and low grade cows: 1980 (70 heifers), 1983 (27 heifers), 1984 (30 heifers), 1985 (30 cows and heifers) and 1990 (16 cows and heifers). By the 1990 mating season there were 200 Brahman breeders on "Belmont" consisting of both high and low grade Brahman content.

2.1.3 Herd management

Adults

The females of all lines were grazed as a single herd apart from a fixed mating period, usually beginning in the first week of December. Prior to 1981 the duration of the fixed mating season was 7 weeks but from 1981 onwards the season was 10 weeks. At the commencement of the mating season each line was divided into families of about 30 cows with one 27 month old, virgin bull. There were usually 4 to 6 families in each line, but in some years as many as 10 families were utilised to accommodate crossbreeding programs. After 1980 at least one bull from the previous year's mating was also used. Pregnancy status was diagnosed by rectal palpation at about 10 weeks after the mating season had concluded. From 1983 there were routine vaccinations of all maiden heifers and mating bulls against vibriosis and leptospirosis.

Calves

In addition to the straight bred calves produced during the study period, first cross (F_1) calves were produced in the following years: 1975-1977 BX were crossed with Africander x Hereford-Shorthorn (HS), 1983-84 reciprocal crosses between HS and Brahman, 1986 Brahman crossed with Charolais and 1990 Brahman crossed with either HS or Charolais.

The first calf born each year was allocated a day of birth of zero. Calves born after this date were allocated a sequential day of birth number. The calving season usually began in September and lasted about 90 days. All calves were reared with their mothers in a single herd except during the mating season.

During the 1970's, pre-weaning experimental treatments (parasite control) involved approximately one third of the HS and BX calf crops. All calves were branded and vaccinated (Hardjo-Pomona and 5-in-1) in February and weaning in April or May.

In 1981 the calf year identification system was altered from the year of calving to the year of branding. Therefore the calves born in 1981 were numbered as the 1982 calf crop.

2.2 Genetic selection procedures

2.2.1 Bull selection

During the 1970's the bulls used for breeding were initially selected at weaning for high weight per age and high tick resistance. A final selection was made on their 18 month weight per age. The 1980 and 1982 HS and BX calf crops were divergently selected for high and low weaning weight per age (Burrow *et al.*, 1991). Selection of males in these years usually resulted in less than 50% of the male calf crop being weighed as yearlings because all culled bull calves were castrated and sold. From 1979 onwards the bulls used for breeding were normally selected for high 18 month weight per age. However, in the following calf crops this selection criterion was modified to fit experimental protocols; 1979, 1983 and 1986 calf crops were selected in an environment where parasites were either controlled (dipping and drenching every 21 days) or not controlled (Frisch and O'Neill, unpublished data). In 1984, 1985 and 1986 the Brahmans were selected for high and for low feed intake (Mackinnon unpublished data). Apart from one HS male, all 1985 HS and BX males were castrated (Frisch and Hunter, 1990a). After 1986 there was increased selection pressure for high tick resistance in the HS. The various bull selection protocols were considered to be of no consequence for the analysis of fixed effects of both growth and fertility.

2.2.2 Cow-culling criteria

All heifers in almost all years were joined at about 26 months of age to calve at 3 years of age. In 1976 and 1977 all heifers were jointed as yearlings and in 1981 some of the purchased Brahman heifers were also joined as yearlings. From 1974 to 1984 the only selection of females in all lines was minimal culling for low fertility (a second consecutive non-pregnant result), cow age (10 years) and gross abnormalities (e.g. severe udder defects) or injury. After 1986, HS cows that were highly susceptible to BIK and/or cattle tick were usually culled.

While the criteria for Brahman females remained unchanged throughout the study period the culling criteria for HS and BX were modified. In the years immediately following the 1982/83 drought the number of breeding cows in the HS and BX lines was reduced to 90 and 100 animals respectively. Initially this was achieved by culling cows that were empty at pregnancy diagnosis. This was again modified in 1986 to retain those non-pregnant cows of high age-adjusted weight at 18 months whose progeny were also of high age-adjusted weight at 18 months. Non-pregnant HS cows were also retained if both the cow and her progeny demonstrated high levels of stress resistance, particularly BIK and tick resistance. During these years the percentage of non-pregnant HS and BX cows retained was not more than 5% of the total number of cows in the lines. By 1990, the numbers of breeding cows in the HS and BX lines were 115 and 110 respectively.

The cow-culling procedures in the HS, in the final 5 years of the dataset were aimed at increasing the level of resistance in this genotype to tropical stress without adversely affecting their fertility. By 1990, the HS was no longer regarded as a line representing the European *Bos taurus* but rather a tropically adapted *Bos taurus* (Frisch and O'Neill, unpublished data). As with the protocols for the selection of mating bulls, the various cow-culling procedures were considered to be of no consequence for the fixed effect analysis of both growth and fertility.

2.3 The datasets

Two datasets, one for growth performance of calf crops and the other for female fertility, were generated from the "Belmont" database utilising data from the HS, BX and Brahman lines.

2.3.1 Growth

The dataset contained records from 3414 calves from the HS, BX and Brahman lines, born from 1974 to 1990. Each record consisted of: year of birth (or, after 1981, year of branding), genotype, sex, calf day of birth, live weights at birth, weaning, yearling and a final weighing at about 18 months of age, and the age (days) of calf at weaning, yearling and the final weighing. Pedigree information for each calf included sire and dam number and the dam's age and previous lactational status (maiden, lactating, non-lactating and non-lactating due to loss of calf).

The following additional variables were incorporated into the Brahman line; Brahman content of calf and source ("Belmont" or industry) of sire and dam. Brahman calves born on "Belmont" ranged in grade from 5/8th Brahman content to purebred (63/64th). Calves equal to or below 5/8th content were removed from the dataset.

A record was also removed from the dataset if the calf was born outside the normal calving season, from embryo transfer, a twin, orphaned or castrated. Records of calves treated for parasites or given hormonal growth promotants were removed. If an animal had been affected by either Lantana poisoning or Bovine Ephemeral Fever, all subsequent weights were removed.

The female calf crop was present for all weighings in all years. The complete male calf crop was present for birth and weaning weights only. In 1979, 1983, 1984 and 1986 onwards the completed male calf crop was also present for the yearling and final weighing. For the remaining years, the males left entire were retained in the dataset but all castrated males were removed before the yearling and final weighings. The absence of the complete male calf crop in these years resulted in a variation in the number of calves between years.

The growth dataset did not include a potential source of variation brought about by families in different locations during the 7 or 10 week mating period. Fitting mating families as a main effect of weaning weight would have produced results difficult to interpret because of the small number of observations per family in most years. In addition there was always complete confounding between breed and paddock.

2.3.2 Fertility

Reproductive data from the HS, BX and Brahman lines from 1974 to 1990 were extracted from the "Belmont" Database to make up a 8130 record dataset. A record on each female of breeding age consisted of the following information; genotype, cow day of birth, mating family, live weights at the start and end of the breeding season, duration of the breeding season (days), pregnancy diagnosis (pregnant, non-pregnant), year of pregnancy diagnosis, cow age (years), previous lactational status (maiden, lactating, non-lactating and non-lactating due to loss of calf) and, for lactating cows, the day of calving where day zero was the day the first calf was born in each calving season and is equivalent to the calf day of birth in the growth dataset.

Data from females involved in experiments that resulted in a significant ($P<0.05$) difference in pregnancy rates, when compared with control animals in the experiment, were removed from the fertility dataset. These experiments were predominantly associated with studies of endocrinology. Cows that grazed irrigated pasture in the 1982/83 drought mating and/or raised F_1 calves in that mating season (Frisch *et al.*, 1987) were also removed. In this study, grazing irrigated pasture had a significant positive effect on fertility and nursing F_1 calves had a significant negative effect on fertility. Cows of the three lines raised F_1 calves in other years but there was not a significant (P>0.10) difference between the pregnancy rates of these dams and dams that raised straightbred calves. Cows with calves born out-of-season were likewise removed from the dataset. As with the growth dataset, not all years involved cows in treatment groups being removed from the dataset and, thus, there was a large variation between years in the numbers of animals.

Data from 1978 and 1979 were excluded from the fertility analysis because of the conditions under which they were collected. The summer flood of 1978 was so severe that the mating season was reduced to 3 weeks duration. This short mating season resulted in an abnormally low pregnancy rate in 1978 and an abnormally high proportion of non-lactating cows, as well as lactating cows with early born calves, being joined in 1979.

Data from mating families with a pregnancy test result of less than 20% were removed from the dataset as the bulls of these families were considered sub-fertile. Fourteen mating families were removed for this reason.

The registered Brahman females that were purchased from industry herds were assigned a "Belmont" equivalent day of birth based on the date of birth on their registration certificate. Because the date of birth of unregistered females from industry herds was unknown the data from these females were excluded from the dataset until their third breeding season.

2.4 Statistical analysis

Harvey's PC version of Mixed Model Least Squares and Maximum Likelihood (Harvey 1987) was used to analyse both the growth and fertility data. Model 1 of the version was used to partition the variance into fixed effects, interactions and covariates. As the datasets consisted of unequal sub-class numbers, due consideration was given to non-orthogonality and model selection (O'Rourke, 1986). Where possible, cells were combined in an effort to balance sub-class numbers. Furthermore, non-significant terms were removed from the final models because their retention would have inflated the variances of other terms (Shepherd, 1986). The assumption that a variable is normally distributed before an analysis of variance is undertaken (see Freund and Walpole, 1987) was not violated for growth data but there was violation for binary reproductive data. However Shepherd (1986), using a fertility dataset that was similar to the one in the present study, has shown that a least squares analysis of variance is highly robust for such binary response data. Hence, the relatively simple least squares analysis of variance was chosen for the analysis of both the growth and fertility datasets from "Belmont". Nevertheless, for any further refinement of the models of reproductive data, use of a more complex analysis, such as a logit analysis, is recommended (Nicholls and Tyrrell, 1980).

2.4.1 Dependent variables

Growth

The dependent variables used in the least squares analyses of the growth dataset were calf day of birth (CBDAY), calf live weight at birth (BWT) and three calf age-adjusted weights. The age adjusted weights were calculated as follows:

WWT = (weaning weight/age of calf) x 200 days

YWT = (yearling weight/age of calf) x 365 days

FWT = (final weight/age of calf) x 550 days

Fertility

The dependent variables used for the fertility model included pregnancy success (1 = pregnant, 0 = non-pregnant), the heifer's day of birth (HBDAY), cow live weight at the start of the breeding season (IWT) and the daily weight gain of the cow during the breeding season (MWGD) and for lactating cows, day of calving (DAYOC).

2.4.2 Fixed effects

Environmental categories

As a means of studying the performance of beef cattle in environments that vary between years, a number of researchers (Vernon *et al.*, 1964; Frisch *et al.*, 1987; Itulya *et al.*, 1987; De Nise *et al.*, 1988) have allocated years into "good" and "poor" environmental categories. To estimate genetic parameters for preweaning characteristics of beef cattle in different environments, De Nise *et al.* (1988) partitioned 29 years of data into three environmental categories (poor, moderate and good) based on weaning weights over those years. Similarly, Frisch *et al.*(1987) allocated calf crops over 11 years at "Belmont" into categories either above or below the overall mean calf crop of 51%. In this way the authors of both studies were able to classify "good" (relatively low environmental stress) and "poor" (relatively high environmental stress) years in terms of performance and investigate the responses of different parameters to the different environmental categories.

In the present study, environmental category, rather than years was used as a fixed effect.

In this study, a least squares mean was calculated for the four growth variables for each calf crop. Each calf crop was allocated into an environmental category either above (defined here as "good" years) or below (defined here as "poor" years) the overall least squares mean for the variable. The allocation of calf crops into two environmental categories for BWT, WWT, YWT and FWT is given in Tables 1, 2, 3, and 4 respectively. The distribution of calf crops into environmental categories was not confounded with the length of the breeding season (7 or 10 weeks), as calf crops from the two lengths of breeding season were represented in both environmental categories.

Environmental category was also used in the analysis of all fertility variables, and was based on pregnancy rate. Partitioning of the fertility dataset into two categories would have resulted in unbalanced data as four years (1976, 1977, 1980 and 1983), were below the overall mean pregnancy rate of 72.2% and the remaining eleven years were above the mean. The data were balanced by partitioning the dataset into three environmental categories. Years where the pregnancy rates were 78% and above were defined as "good" years for fertility, years between 78% and 68% as "average" years and 68% and below were defined as "poor" years. By using pregnancy rates of 78% and 68%, the data for the three environmental categories were not only balanced but also not confounded with length of breeding season (7 or 10 weeks). The allocation of years into the three environmental categories is given in Table 5.

Genotypes

The growth dataset for the HS was derived entirely from calves born to HSS cows. Prior to 1977 no distinction was made between the HSS and HSR lines for the fertility dataset. After 1977, data from HSS cows only was used as this line was then closed.

The data for both growth and fertility from the BX line were derived from F_n animals only as all F_1 animals were removed.

Differences in growth and fertility between "Belmont" and all non-"Belmont" Brahman sires were found to be not significant (P>0.10) and the effect of sire source was ignored. A subset of data from 1980 to 1990 was used to test for any differences between "Belmont" and non-"Belmont" Brahman dams. As with the sires there was no significant difference (P>0.10) between the two sources of dam.

Cows of 15/16th Brahman content may be registered as purebreds with the Australian Brahman Breeders Association whereas cows below this grade are given appendix status in the register. For the purposes of this analysis, Brahman cows and calves that were 15/16th or above were assigned high grade (BH) and below 15/16th were assigned low grade (BL). In 1990 the 21 purchased unregistered Brahmans still on "Belmont" were allocated, on the basis of physical appearance , into either high or low grade status by Mr J.J. Davies, head stockman on "Belmont". Other records from cows of unknown grade were removed from the dataset. The allocation of two grades of Brahman resulted in a total of four genotypes (HS, BX, BL and BH) for both the growth and fertility models.

The BL cows were a mixture of interbred low grade cows and 3/4th backcross cows born to F_1 Brahman x *Bos taurus* cows. Approximately 10% of the females were known to be a Brahman backcross but it was not known how many industry cows were of this genotype. Hence, the heterotic influence on the BL line could not be determined.

Cow age and previous lactational status

The variables of age of cow (AGE) and previous lactation status (PLS) can be analysed as separate fixed effects. However, because there were no lactating 3 year old cows there was confounding between the two variables. Therefore the two variables were combined into a single main effect (AGEPLS), overcoming this confounding. Furthermore, within each PLS class those cow ages that were not significantly different (P>0.10) from each other were also combined. The growth model had the following 5 classes of AGEPLS; 3 year old maidens, lactating cows of 4 and 5+ years and non-lactating cows of 4 and 5+ years. The resulting AGEPLS fixed effect for the fertility model had the following 8 classes; 3 year old maidens, lactating cows of 4, 5, 6, 7 to 9 and 10+ years, and non-lactating cows of 4 and 5+ years. Most non-pregnant cows over 8 years of age were culled and hence the few cows that were retained were not treated as a separate class. Cows that had lost their calf prior to the start of the breeding season were allocated to the non-lactating class.

The initial analysis of the fertility dataset (Table 7) included data from all cows that calved during the calving season. For subsequent analyses of this dataset, those cows whose DAYOC was unknown were removed from the dataset.

The 22 females, of all 4 genotypes, that calved as 2 year olds were retained in the dataset as 3 year olds as it was assumed that had these heifers been given the opportunity they would have calved as 3 year old maidens. The next pregnancy record of these cows was ignored.

Sex of calf

Sex of calf (1=male, 2=female) was fitted as a fixed effect for the growth model. A preliminary analysis of the fertility dataset found sex of calf to be non-significant (P>0.10) and sex of calf was ignored as a fixed effect for the fertility model.

2.4.3 Interactions

Significant 1st order interactions between fixed effects and interactions between fixed effects and covariates were fitted to models of both growth and fertility.

The classes of AGEPLS were modified to illustrate the interactions for fertility. Lactating cows 5 years of age and older were able to be combined into a single age class (5+ year) because the interactions between the various ages were not significant (P>0.10).

2.4.4 Covariates

CBDAY was fitted as a covariate to the growth model and HBDAY, IWT, MWGD and DAYOC were fitted as covariates to the fertility model. These variables are known to have important influences on growth and fertility of beef cattle in a tropical environment (e.g. Frisch *et al.*, 1987).

CHAPTER 3

RESULTS

Results from the analyses of the growth and fertility datasets are partitioned into sections on fixed effects and sections on interactions. Fixed effects for both growth and fertility are environmental category, genotype and the combined effect of cow age and previous lactational status. Sex of calf is presented as a fixed effect for growth. Significant interactions between the fixed effects are then illustrated for both growth and fertility. Unless otherwise stated, statistical significance is taken at $P<0.05$ for all sections. In all tables the letter N denotes the number of observations within each class of fixed effect and "line" is synonymous with genotype.

3.1 Fixed effects

3.1.1 Environmental category

Growth

The overall mean liveweights for birthweight (BWT) and the age-adjusted liveweights at a 200 day weaning weight (WWT), a 365 day yearling weight (YWT) and a 550 day weight (FWT), for both calf crop and environmental category, are given in Tables 1, 2, 3 and 4 respectively. Of the 16 calf crops very few were in the same environmental category at each of the four weighings. Both the 1977 and 1979 calf crops were consistently below the overall mean weight for each of the four variables and the 1986 and 1989 calf crops were consistently above the overall mean for each of the four variables.

Table 1 shows that for BWT most of the calf crops of the 1970's occurred in the poor years category and most of the calf crops of the 1980's occurred in the good years category. Although the difference in BWT between the good and the poor years was only 1.7 kg there was a 5.0 kg difference between the year of highest BWT (1987 calf crop) and the year of lowest

BWT (1977 calf crop).

As with BWT most of the weaning weights from the 1970's were in the poor years category (Table 2). Apart from the 1974 calf crop all the calf crops in the good years category were from the 1980's. The difference in weight between the heaviest weaners (1989 calf crop) and the lightest weaners (1976 calf crop) was 40.6 kg.

The liveweight differences between the two categories for the calf crops as yearlings (Table 3) were similar to the corresponding differences for weaning weight (Table 2). The difference between the good and poor categories for YWT was 16.8 kg with a 41 kg weight difference between the heaviest (1986 and 1989) and lightest (1982) calf crops. The 1982 calf crop was 17.6 kg below the mean of the poor years and 34.4 kg below the mean of the good years.

The largest separation in weights between the two environmental categories was at the final weighing (Table 4). The difference between the good and poor year categories for FWT was 30.0 kg and the largest difference in weight between any two calf crops was 58.2 kg (1986 and 1982 calf crops).

The rates of growth of calves during different growth phases (birth to weaning, weaning to yearling and yearling to 18 months of age) were substantially different. Daily weight gain from birth to weaning was 0.71 kg/day, from weaning to yearling (autumn to spring) was 0.12 kg/day and from yearling to 18 months-of-age (spring to autumn) 0.49 kg/day, 4 times the rate of gain during the weaning to yearling growing phase.

Fertility

The mean pregnancy rate for each year and the partitioning of these into three environmental categories are presented in Table 5. The difference in pregnancy rate between years was highly significant (P<0.001). The pregnancy rate for 1989 (the year of highest pregnancy rate) was over 30 percentage units above the pregnancy rates for 1980 and 1983. The difference in pregnancy rate between the good years and average years was almost 7 percentage units. The corresponding difference in pregnancy rate between average years and poor years was over twice as large at 17 percentage units.

The mean cow liveweight at the start of the breeding season and weight gain per day during the breeding season for each of the environmental categories are also given in Table 5. For both IWT and MWGD, the difference between the means of each environmental category was highly significant ($P<0.001$). The cows within the good years category had the heaviest IWT and the cows in the poor years had the lightest IWT. This trend was not repeated with the daily weight gain of cows during the breeding season. The cows within the good years gained the least weight during the breeding season and cows within the poor years gained the most.

3.1.2 Genotype

Growth

The mean day of calving (CBDAY), the mean BWT, WWT, YWT and FWT for the HS, BX, BL and BH over the 16 calf crops on "Belmont", are presented in Table 6. HS calves were born almost 7 days earlier ($P<0.001$) than BX calves which were born almost 6 days earlier ($P<0.001$) than calves from the two Brahman lines. The BH calves were born last but not significantly ($P>0.20$) later than the BL calves. At each of the four weighings, genotype was a highly significant ($P<0.001$) fixed effect but no single genotype consistently weighed the heaviest or lightest at all of these weighings. The HS calves were over 3 kg heavier at birth ($P<0.001$) than the BH calves. The BWT's of BX and BL calves were almost identical to one another and were significantly ($P<0.001$) heavier than the BWT for BH calves. The WWT of the BX calves was significantly heavier than that of BH calves. The BL calves weaned 4.2 kg heavier than the BH calves but this difference was not significant ($P>0.10$). The BX and BL were the heaviest weaners and the difference in weight between these two lines at weaning was not significant (P>0.20). Difference in growth between the BX and BL did not occur until YWT (P=0.01) and remained at FWT (P=0.06). As BX and BL became dissimilar, the similarity between the BL and BH increased. By the final weighing the two Brahman lines were heavier (P=0.06) than the BX and not significantly different from each other (P>0.20). The HS had the lowest weight at each age after birth and by FWT the HS were over 60 kg (P<0.001) behind the BL and BH.

Fertility

Genotype significantly (P<0.001) affected overall mean pregnancy rate (Table 7). There was a difference of 5 percentage units between the genotypes of highest pregnancy rate (HS and BL) and the genotype at the intermediate level (BX) for pregnancy rate. The corresponding difference in pregnancy rate between the highest and lowest (BH) genotype was 15 percentage units.

3.1.3 Age and previous lactational status of cow

Growth

The mean CBDAY and calf birth weight, as well as calf age-adjusted weights at weaning, yearling and 18 months for each class of the combined effects of the dam's age and previous lactational status are given in Table 8.

Three year old maidens and cows that had been non-lactating the previous year calved significantly (P<0.001) earlier than cows that were lactating the previous year. The earliest calving cows (5+ year old non-lactating) calved almost two weeks before the last calving group (4 year old lactating) (Table 8).

AGEPLS was a highly significant (P<0.001) fixed effect for BWT, WWT, YWT and FWT. In general, calves born to cows 5 years and older were heavier than calves born to younger cows. Superimposed on the effects of dam age were the effects of the dam's previous lactational status. Calves born to cows that were non-lactating the previous calving season were usually heavier than calves whose dams had raised a calf the previous season (except for 4 year olds, see below). Table 8 shows the general consistency of rankings of the growth of calves born in the different AGEPLS categories. Calves born to 3 year old maidens consistently had the lowest growth rates while calves born to non-lactating cows 5 years and older were heaviest. In particular, the BWT of calves from 3 year old maidens was significantly less than the BWT of calves from other cows. Although the differences in calf growth between the maidens and 5+ year old non-lactating cows was largest at weaning (14.8 kg) there were still highly significant ($P<0.001$) differences between the two classes at YWT (7.8 kg) and FWT (10.9 kg). The consistent advantage in calf growth provided by the 5+ year old non-lactating cows was still evident when the calves were 18 months of age. Calves from this group of cows had a significant (4.8 kg) weight advantage over calves born to lactating cows of the same age group and about 11 kg ($P<0.001$) advantage over calves from 3 and 4 year old cows.

However, the 4 year old non-lactating cows were somewhat of an enigma. Calves from this group of cows did not receive the advantage that would be expected from the above results (Table 8). Calves from 4 year old non-lactating cows were born significantly ($P<0.01$) later than calves from the other non-lactating classes. Their weights were sometimes less (eg. YWT, $P<0.10$) although usually not significantly different overall ($P>0.20$) from the weights of calves from their 4 year old lactating contemporaries.

Fertility

The means for pregnancy rate, IWT, MWGD and DAYOC for each class of AGEPLS are presented in Table 9.

Three year old maidens and 5+ year old non-lactating cows had similar ($P>0.20$) and significantly higher pregnancy rates than all other classes of AGEPLS. The maidens were almost 33 percentage units higher in pregnancy rate than the 4 year old lactating cows. However, during the breeding season the 3 year old maidens grew significantly faster (P<0.01) than any other age group. The age classes of lactating cows show a saw-tooth effect for pregnancy rate. Peaks in pregnancy rate occurred at 5 years and 7-9 years while troughs occurred at 4 years, 6 years and 10+ years (Table 9). The most fertile lactating cows were aged 7-9 years, although not significantly different from the 5 year olds (P>0.20) but were significantly more fertile than 4 year old (P<0.001), 6 year old (P<0.05) and 10+ year old (P<0.01) lactating cows.

The above patterns in pregnancy rates are not reflected in the IWT and MWGD of the classes of AGEPLS (Table 9). The 3 year old maidens had the lowest (P<0.001) IWT, but the highest (P<0.01) MWGD, of any class of AGEPLS. At the start of the breeding season, the maidens were 37 kg lighter in body weight than the next lightest group, the 4 year old lactating cows. Maidens had significantly higher (P<0.001) MWGD than both the 4 and 5+ year old non-lactating cows. For lactating cows there was a significant increase in IWT with increasing age as the cows approached the age of 10 years. On the other hand, MWGD was consistently around 0.18 kg/day for all lactating cows, which was about ⅓ of the daily weight gain of maidens and non-lactating cows. Although the pregnancy rate dropped significantly from 10 years of age onwards, IWT and MWGD remained very similar to the values for the 7-9 year old group.

DAYOC was longest for 5 year olds, significantly longer than for 4 (P<0.01) and 6 year old cows (P<0.05). As with MWGD of lactating cows, both the 7-9 year olds and 10+ year olds had very similar (P>0.20) DAYOC (Table 9).

Fertility of maiden heifers

Table 10 presents the mean pregnancy rate and mean pregnancy rate adjusted for HBDAY and IWT for 3 year old maidens of each genotype. The means for HBDAY, IWT and MWGD are also shown.

Although there was no significant difference ($P>0.20$) in reproductive rate between any of the genotypes there was a significant ($P<0.01$) difference in HBDAY and IWT with the HS being the oldest and lightest (Table 10). Simultaneously adjusting pregnancy rate for the differences in HBDAY and IWT increased the fertility of HS maidens and decreased the fertility of both BL and BH maidens ($P<0.06$).

Fertility of lactating cows

The fertility of lactating cows differed markedly between genotypes (Table 11). The HS line was significantly more fertile ($P<0.01$) than all other lines and 21 percentage units higher ($P<0.001$) than the least fertile line, the BH. There was no significant difference between the BX and BL ($P>0.20$) and these two genotypes were significantly ($P<0.01$) more fertile than the BH.

There were large and highly significant differences between the genotypes for IWT, MWGD and DAYOC (Table 11). The HS had significantly ($P<0.001$) lower IWT than all other genotypes and were almost 49 kg less than the BL, the line with the highest IWT. The BX and BL did not differ significantly ($P>0.10$) in IWT and both were significantly ($P<0.001$) heavier than the BH. The HS, BX and BL cows had identical or similar MWGD ($P>0.10$). However, the MWGD of BH was not only close to zero but also highly significantly lower ($P<0.001$) than that of the other 3 genotypes. As well as having the lowest MWGD the BH also had the highest DAYOC. On average, cows of the BH line calved almost 2 weeks later than the HS cows ($P<0.001$). The 3 days difference in DAYOC between the high and low grade Brahman lines was not significant ($P>0.10$).

Simultaneously adjusting pregnancy rate for differences in IWT, MWGD and DAYOC did not entirely remove the differences in fertility between the *Bos indicus* derived genotypes but reduced it to a low level of significance. However the adjustments increased the difference between HS and other genotypes (Table 11).

The mean pregnancy rate, IWT and MWGD for lactating cows are presented in Table 12. The difference in pregnancy rate between good and average years was 10 percentage units and between average and poor years was 25 percentage untis. In the years of high pregnancy rate lactating cows weighed heaviest and gained the least weight during the breeding season and conversely, in poor years they weighed lightest but had the highest MWGD.

Fertility of non-lactating cows

The mean pregnancy rate both alone (74.7%) and adjusted for MWGD and the means of IWT and MWGD for non-lactating cows of each genotype are given in Table 13.

The fertility of non-lactating cows was significantly affected by genotype. Both the HS and BX genotypes were significantly more fertile than the BH ($P<0.01$) but not BL ($P>0.20$). The pregnancy rate for the BL was 8 percentage units higher than that of the BH but this difference was not significant ($P>0.10$).

IWT and MWGD were both dependent on genotype ($P<0.001$). Both the BX and BL were 22 kg ($P<0.01$) heavier than the BH and 46 kg ($P<0.001$) heavier than HS (Table 13). The 24 kg difference between HS and BH was also highly significant ($P<0.001$). Although the HS cows had the lowest IWT they gained more weight than the BX and both of these genotypes significantly ($P<0.001$) outgained the Brahman lines. The difference between the two grades of Brahman was not significant ($P>0.20$).

3.1.4 Sex of calf

Growth

Male calves were born 2.0 days later ($P<0.01$) and 2.6 kg heavier ($P<0.001$) than female calves (Table 14). The growth advantage of males compared to females was highly significant ($P<0.001$) and was maintained at all weighings. Although the difference between the sexes was similar for

WWT and YWT (14.0 kg and 14.9 kg respectively) the difference increased to 23.7 kg by FWT.

3.2 Interactions

3.2.1 Genotype by environmental category

Growth

The interaction between genotype and environmental category was significant for BWT ($P<0.01$), WWT ($P<0.001$), YWT ($P<0.01$) and FWT ($P<0.01$). Illustrations of the interactions are presented in Figures 1, 2, 3 and 4 respectively.

Figure 1 shows that in both categories the HS calves were born heaviest and BH calves were born lightest. The significance of the interaction for BWT was primarily due to the relatively small difference in BWT, between the good and poor years for BX (1.2 kg) compared to the corresponding differences for HS (2.0 kg), BL (2.1 kg) and BH (2.7 kg).

The pattern of interaction between genotype and environmental category was very similar for the remaining 3 growth variables (Figures 2, 3, and 4). In the good years the BX calves consistently weighed the heaviest whereas in poor years the BL was consistently the heaviest. In the poor years the BL calves were significantly ($P<0.001$) heavier at weaning than the BH calves. However, by FWT the difference in weight between the two Brahman lines had been reduced to non-significance ($P>0.20$).

The other consistent pattern in the above interaction for WWT, YWT and FWT was the difference in weight between good and poor years for each genotype. The difference between good and poor years was greatest for the HS and BX calves and least in BL calves with BH calves being intermediate. For BL calves the differences in WWT and YWT between good and poor years, were only 0.2 and 1.1 kg respectively.

Fertility

The interaction (P<0.05) between genotype and environmental category for pregnancy rate is presented in Figure 5. In good years the increasing *Bos taurus* content of the genotype was associated with increasing pregnancy rate. In both good and average years the HS had the highest pregnancy rate and the BH the lowest pregnancy rate. In good years the BX had a higher pregnancy rate than the BL but this ranking was reversed in average and poor years. In poor years the pregnancy rate of the HS dropped to equal that of the BX but the pregnancy rate of the BL remained relatively high.

The highly significant (P<0.001) interaction between genotype and environmental category for IWT is presented in Figure 6. In all environmental categories, the BL were consistently the heaviest at the start of the breeding season. Although the BH were heavier than HS in the three categories, the drop in IWT of the BH (60.1 kg), from good to poor years was twice the corresponding drop of the HS (30.6 kg) (P<0.001). The drop in IWT from good to poor years for BX and BL was 47.0 kg and 45.7 kg respectively.

The BH not only exhibited the largest drop in IWT between the environmental categories, but also consistently gained least weight during the breeding season in all three categories (Figure 7). The interaction between genotype and environmental category was also highly significant for MWGD (P<0.001) (Figure 7). The difference in MWGD between BL and BH was least for good and average years and greatest for poor years.

3.2.2 Genotype by AGEPLS

Growth

Of the four growth variables studied, WWT was the only variable for which there was a significant interaction between AGEPLS and genotype (Figure 8). Between the five classes of AGEPLS the differences (P<0.01) in calf WWT were greatest for HS and BX, and smallest for BH. The greatest differences in AGEPLS occurred between calves from 3 year old maidens and

5+ year old non-lactating cows for both HS (21.8 kg) and BX (20.2 kg) lines. The corresponding differences for BL and BH were 11.3 and 5.8 kg respectively.

Fertility

As shown previously in this chapter (Tables 9 and 10), pregnancy rates of three year old maidens were consistently high and similar across all genotypes. The pregnancy rates of the two non-lactating classes of AGEPLS were also similar to each other and consistently high for all genotypes except BH (Figure 9). The non-lactating BH were on average 11 percentage units below non-lactating contemporaries of the other lines.

On the other hand there were large genotype differences in the fertility of the two lactating classes ($P<0.01$) (Figure 9). The pregnancy rates of 4 and 5+ year old lactating HS cows were similar, unlike the corresponding pregnancy rates in the other three genotypes. For lactating BH cows, not only was the pregnancy rate the lowest but also the difference in pregnancy rate between 4 and 5+ year old cows was the greatest. In particular, the contrast between 3 year old maidens and 4 year old lactating cows was significantly ($P\leq0.05$) greater in these two classes than for all other genotypes.

The interactions between AGEPLS and genotype were not significant for both IWT ($P=0.10$) and MWGD ($P>0.10$).

3.2.3 AGEPLS by environmental category

Growth

Calf growth rates, from birth to 18 months of age, were influenced by both age and previous lactational status of the dam. However, the interaction between AGEPLS and environmental category was significant only at the final weighing. Figure 10 shows that the influence of AGEPLS on FWT in good years was minor compared to the influence in poor years. In poor years, calves raised by 3 year old maidens or lactating cows were relatively more disadvantaged than calves raised on older or non-lactating cows. In the poor years, calves reared by non-lactating 5+ year old cows were heavier than those reared by both lactating 5+ year old cows and by 3 year old maidens (differences of 10.3 and 18.4 kg respectively).

Fertility

There were significant interactions between AGEPLS and environmental category for pregnancy rate ($P<0.001$), IWT ($P<0.01$) and MWGD ($P<0.01$).

Three year old maidens and 5+ year old non-lactating cows achieved relatively high and similar, pregnancy rates in all three environmental categories (Figure 11). The 4 year old lactating cows had significantly lower pregnancy rates than maidens and 5+ year old non-lactating cows, in good, average ($P\leq0.01$) and poor ($P<0.001$) years. Lactating 5+ year olds experienced a large drop in pregnancy rate in poor years. The pregnancy rate of non-lactating 4 year olds also declined in poor years but not to the same extent as occurred in lactating cows.

The interaction between AGEPLS and environmental category for IWT is presented in Figure 12. Differences in IWT between good and average years were significantly larger for older cows (33 kg) than for cows that were 3 or 4 years old (20 kg). On the other hand, the difference in IWT between average and poor years were minor for the two non-lactating classes (8 kg) when compared to 3 year old maidens and lactating cows (21 kg).

The interaction between AGEPLS and environmental category for MWGD is presented in Figure 13. MWGD increased in all five classes of AGEPLS from good to poor years. However, the increase weight gain of 3 year old maidens and non-lactating cows was minor and significantly ($P<0.01$) less than the corresponding increase in the weight gain of lactating cows.

3.2.4 Genotype by sex of calf

Growth

The interaction between genotype and sex of calf has been demonstrated by plotting the difference in weight between male and female calves for each genotype at birth, weaning, yearling and 18 months of age (Figure 14). The interaction of genotype by sex was significant for BWT and highly significant (P<0.001) for WWT, YWT and FWT.

Males of the BX, BL and BH lines were born about 3 kg heavier than their respective females while HS males were born only 1.8 kg heavier than HS females. In general, for the Brahman derived genotypes, there was an increase in the difference in weight between the sexes at each weighing after birth. The difference between the sexes was greatest at the lowest level of *Bos indicus* content. The corresponding weight differences for HS remained small.

3.3 Covariates

3.3.1 Growth of calves

The regression of CBDAY on each of the four growth variables was highly significant (P<0.001), however the sign of the slope of the regression altered between the four variables (Table 6). The regressions for the two variables associated with maternal effects (BWT and WWT) were positive and for the two post-weaning variables (YWT and FWT) were negative. Whereas the regression at birth was positive and small, the regression at weaning was positive but relatively large. The large negative regression of the first post-weaning weighing (YWT) reduced in magnitude by the final weighing (FWT). Interactions between CBDAY and the main effects, environmental category, genotype, sex and combined effect of age of dam and the previous lactational status of the dam were not significant (P>0.10 in all cases).

3.3.2 Fertility of maidens

The within genotype regressions of percentage pregnant of three year old maidens on HBDAY and IWT are shown in Table 10.

The regressions were significant for HBDAY and IWT but not for MWGD (Table 10). The regression on HBDAY indicated that the younger HS maidens were more fertile than the older HS maidens, while younger BL and BH maidens are less fertile than the older maidens of these lines. The corresponding regression on IWT showed a similar separation of the genotypes. Although the common regression of pregnancy rate on IWT (b = 0.12±0.039%) was significant, not all genotypes displayed the same magnitude of response. The BX showed no response, the HS and BL an intermediate response, while the BH response was relatively large and highly significant (P<0.01). The differences in MWGD between the four genotypes were either zero or very small (P<0.10).

3.3.3 Fertility of lactating cows

Table 11 also presents the regression coefficients for pregnancy rate for lactating cows on each variable used to adjust pregnancy rate. As well as the common regression of percentage pregnant on IWT (b = 0.14±0.018%) being highly significant (P<0.001), the regression between environmental categories was also significant (P<0.01). The within environmental category regression was significant because of the relatively small effect of IWT in the good years and its relatively large effect in poor years. In good years, increasing IWT by 50 kg would increase the pregnancy rate by only 4 percentage units, but in poor years the corresponding response in pregnancy rate would be almost 10 percentage units.

The regression co-efficient for pregnancy rate on MWGD was also highly significant (P<0.001) and acted equally within each environmental category (P>0.20) (Table 11). The effect of MWGD was however, small in that for every 1 kg/day increase in MWGD there would only be a 9 percentage unit increase in reproductive rate. A realistic daily gain in weight is unlikely to exceed 1 kg/day and if lactating cows were to achieve 1 kg/day this would only bring about an additional 6 percentage units in pregnancy rate.

The regression co-efficient for pregnancy rate on DAYOC was negative and highly significant (P<0.001) (Table 11). The later in the season a cow calved, the less likely she would conceive during the following breeding season. For every additional day of DAYOC the reproductive rate of cows would drop by 0.17%, that is, for each 30 days (⅓ of the breeding season) calving rate would decline by about 5 percentage units.

3.3.4 Fertility of non-lactating cows

The regression co-efficient of pregnancy rate of non-lactating cows on MWGD is presented in Table 13.

The regression co-efficient of pregnancy rate on IWT was not significant (P>0.20). However, the regression of pregnancy rate on MWGD was highly significant (P<0.001) (Table 13). If non-lactating cows could gain 1 kg/day during the breeding season the response in pregnancy rate would be about 7 percentage units, this being similar to the response for the lactating cows. Adjusting the pregnancy rate of non-lactating cows for MWGD removed most of the differences (P=0.07) in pregnancy rate between the lines.

CHAPTER 4

DISCUSSION

The major, non-genetic facotrs that affect both the growth and reproductive rates of cattle, in tropical environments, have been largely documented. However, some critical aspects of the factors that affect growth and fertility in a dry tropical environment have not been addressed by previous studies. The present study is an investigation of the appropriate dependent variables, fixed effects, interactions and covariates that are components of models of both the growth and fertility of beef cattle in a dry tropical environment. The discussion of the results will focus on the factors that have been given little attention in previous studies.

A number of researchers are concerned that aspects of the new animal breeding technologies, designed for use in temperate beef production systems, do not adequately reflect the genetics of beef production in the tropics (Hetzel *et al.*, 1990; Notter and Hohenboken, 1990; Robinson and O'Rourke, 1992; Davis, 1993). Because of these concerns, the discussion will highlight implications for the genetic improvement of productivity for tropical environments. In particular, the within-breed genetic improvement will be examined in terms of models that account for the variation in both environments and genotypes of the tropics. Its location (latitude 23°S) in northern Australia and the management procedures employed on the property have ensured that data from "Belmont" resembles that of the northern beef industry. The production system on "Belmont" has been defined as follows: a fixed breeding season, calving heifers first as 3 year olds, spring calving season, growing cattle on pasture and no routine control of parasites, supplementary feeding or early weaning, or the use of metabolic agents. The discussion of the dependent variables, fixed effects, interactions and covariates derived from analysis of the data will be given in terms of this production system. Use of environmental categories (good verses poor years) has enabled the findings from the dry tropical environment of "Belmont" to be extrapolated to other tropical environments where the level of environmental stress is either relatively lower or higher than that of "Belmont".

4.1 Dependent variables

The appropriate traits for the production system and genotypes used on "Belmont" were birth weight (BWT) and age-adjusted liveweights at 200 (WWT), 365 (YWT) and 550 (FWT) days of age for growth, and pregnancy rate for fertility.

4.1.1 Birth weight

The BWT's of calves on "Belmont" ranging from a low of 28.7 kg in 1977 to a high of 33.7 kg in 1978 (Table 1), would generally be regarded as moderate and there is ample evidence that a moderate BWT is also an optimum BWT (see Preston and Willis, 1974). Birth weights that are above these weights contribute significantly to dystocia, especially when associated with young cows (Azzam *et al.*, 1993; Basarab *et al.*, 1993). The incidence of mortalities from dystocia on "Belmont" was low, about 1% per year for the duration of the study period (pers. comm. Mr. G. Halford, Manager of "Belmont"). This observation is in agreement with studies of dystocia in the tropics (see Preston and Willis, 1974; Trail *et al.*, 1977).

Whether or not the incidence of calf mortalities in general, and dystocia in particular, remains low, depends upon the genetic trend in BWT for the various genotypes on "Belmont". Because of the association of extremes in BWT with reduced productivity (Bellows and Short, 1978; Morris *et al.*, 1986; Newman and Deland, 1991; Turner and Farnsworth, 1993), the genetic trend in BWT should be continually monitored. Monitoring BWT is also desirable because of the positive relationship between selection for increased liveweight at any given age and increased liveweight at all other ages (see reviews by Baker and Morris, 1984; Mrode, 1988). Table 15 suggests that BWT of all genotypes may have increased on "Belmont" but this increase could be larger in the BX and Brahman than in the HS. Since 1974, and up until 1993, the genetic trend in BWT of the HS and Brahmans (combined BL and BH lines) from the within-herd BREEDPLAN analysis of the "Belmont" data was +0.08 and +0.16 kg/year respectively (O'Neill, unpublished). Even under the low levels of selection intensity for high FWT, that are practiced on "Belmont", the *Bos indicus* genotypes in particular, are increasing their BWT's. Any genotype that is relatively adapted to environmental stress and is being selected for high growth rate would simultaneously be selected for high growth potential and therefore high BWT. An increasing BWT would inevitably lead to an increasing incidence of dystocia in the population. Hence, any population in a genetic improvement program for growth should have BWT continually monitored (e.g. using the model proposed by Manfredi *et al.*, 1991), but at present EBV's for BWT are not one of the variables chosen for analysis in Brahman GROUP BREEDPLAN (Anonymous, 1993,1994).

Recording the BWT of Brahmans and generating EBV's for BWT will also be particularly useful for those beef producers using Brahman bulls over *Bos taurus* cows as a crossbreeding option. In this way, the dystocia due to high BWT, that is observed from this crossbreeding option (Smith and Hearnshaw, 1981; Frisch *et al.*, unpublished) may be greatly reduced or at least kept to a manageable level. This supports the contention that BWT should be incorporated into Brahman GROUP BREEDPLAN.

4.1.2 Weaning weight

Whereas BWT has not been chosen as a trait for either tropical EBV's or for Brahman GROUP BREEDPLAN a weaning weight at 200 days is in the present analysis from AGBU (Schneeberger *et al.*, 1991). Weaning at this age is compatible with the production system on "Belmont" and most beef production enterprises of northern Australia. For these reasons, the present study dealt with a 200 day weaning weight and hence the significant fixed effects, interactions and covariates that have been identified are pertinent to this relatively late weaning age.

Weaning calves at substantially earlier ages (e.g. at 100 days or once the calf has reached a minimum liveweight of 50 kg) has been advocated by some workers as a means by which both, the reproductive rates of lactating cows can be increased and cow mortalities reduced (Harwin and Lombard, 1974; Lasby *et al.*, 1981; Boorman and Hosegood, 1986; Schlink *et al.*, 1988; McSweeney *et al.*, 1993). Indeed, a majority of producers in northern Australia have expressed a willingness to wean early when seasonal conditions are poor (O'Rourke *et al.*, 1992). However, compared to a 200 day weaning, calves that are weaned at 100 days are placed in a post-weaning environment such that the productivity of the early weaned calves can be substantially reduced (McCosker *et al.*, 1984; Holroyd *et al.*, 1990c; Schlink *et al.*, 1994). It remains to be seen if the fixed effects, interactions and covariates, identified in the present study, can be transfered to an early weaning system.

4.1.3 Post-weaning weights

In the production system used on "Belmont", YWT incorporates post-weaning growth to the end of the dry season (i.e. September/October). The low growth rates (0.12 kg/day), reflected in YWT's not much greater than the WWT's (Tables 2 and 3), and these are typical of other locations in northern Australia (Holroyd *et al.*, 1990a,b; Hunter and Buck, 1992; Davis, 1993). It has been established that the low rate of growth is an indication of the high levels of environmental stress experienced by weaners during the dry season in northern Australia (Graham *et al.*, 1983; Foster and Blight, 1984; Frisch and Vercoe, 1984;

Boorman and Hosegood, 1986; Taylor *et al.*, 1991).

AGBU currently uses a 400 day weight as a measure of YWT (Schneeberger *et al.*, 1991). In southern Australia, a 400 day weighing (November/December) is more than adequate because this region does not experience distinct dry and wet seasons to the same extent as northern Australia. A 400 day weighing in northern Australia, can mean that the cattle are either weighed after the wet season has commenced or, if the break in the season is delayed, at the end of the dry season. In northern Australia, a 365 day weight (September/October) is a weight at the end of winter. Weighing cattle one or two months later (i.e. at 400 days) can be critical because the summer wet season (high temperatures and high rainfall) has usually commenced and nutritional stress has been largely removed. If, however, the wet season is delayed the 400 day weighing can be taken when nutritional stress is still high. Hence, a yearling weight at 365 days provides a measure of the growth performance of cattle when environmental stress, especially nutritional stress, is usually most consistent and highest.

FWT was taken when the calves were 550 days old and this weighing coincided with the end of the wet season on "Belmont". The overall 550 day weight of 283 kg (Table 4) and the wet season daily rate of weight gain of 0.49 kg/day are comparable to values from other studies in the tropics of Australia (Davis, 1993; Arthur *et al.*, 1994). However, a weighing at 600 days, currently used by AGBU for northern Australia (Schneeberger *et al.*, 1991; Anonymous, 1994), coincides with the middle of the animals' second dry season (June/July). Whereas use of a 550 day weight would be a measure of the animals' growth performance during the wet season, the 600 day weighing is a mixture of the animals' performance during the first wet season and the start of the second dry season. The genes that control the performance of growth in the dry season may either be different from, or antagonistic to, the genes that control the performance of growth in the wet season. If this is the case, a weighing date that encompasses the growth rate for both the wet and dry seasons may prevent or diminish genetic improvement in growth in either season. Alternatively, weighing dates to coincide with the end of the first dry season (365 days) and the end of the first wet season (550 days) would enable genetic improvement programs to target separately the growth performance from weaning to yearling, when nutritional stress is relatively high, and growth performance from yearling to final weight, when nutritional stress is relatively low. In northern Australia, the use of 550 day EBV's, rather than 600 day EBV's, is also supported by Barwick *et al.* (1992). These authors found that the predicted genetic gains in growth were greater for 550 day EBV's than for 600 day EBV's.

4.1.4 Pregnancy rate

As with growth, the choice of appropriate dependent variables for fertility is critical for the genetic evaluation models of fertility. Testing cows for their pregnancy status at the end of each breeding season provided an annual pregnancy rate for "Belmont". The pregnancy rate ranged from 42.9% in 1980 to 85.5% in 1989 (Table 5), and this range is in general agreement with herds of northern Australia (see Reid, 1990). The overall pregnancy rate on "Belmont" during the study period was 72% which is intermediate between the relatively high rates from the sub-tropics and the low rates from the wet tropics (see reviews by Galina and Arthur, 1989a,b,c). The lower reproductive rate of 51% over an eleven year period (years 1973 to 1983), reported in an earlier study on "Belmont" (Frisch *et al.*, 1987), can be partially attributed to the predominance of drought years in this dataset. The lower reproductive rate reported by Frisch *et al.* (1987) can also be explained by the choice of dependent variables. The index of fertility chosen in this study was calving rate rather than pregnancy rate, and the calving rates would be expected to be lower due to pre-natal losses.

As pre-natal loss in cattle are known to be caused by stress, high ambient temperatures and deficient nutrition (see Hungerford, 1990) relatively high rates of pre-natal mortality can be expected to occur in the tropics where the level of environmental stress is high (see Entwistle, 1983). In northern Australia when pre-weaning calf mortalities are combined with pre-natal losses, the total post-conception losses up to weaning can range from 6% to 70% (see Entwistle, 1983). A similar range in post-conception losses has been reported in other tropical locations (see Galina and Arthur, 1989c). As rates of both embryonic and calf survival, and factors affecting these survival rates, were considered beyond the scope of the present study, the trait chosen as the dependent variable for fertility was pregnancy rate.

The yearly variation in pregnancy rate on "Belmont" (Table 5), and at other locations in northern Australia (Anderson *et al.*, 1988; Holroyd *et al.*, 1990a,b), suggests that days to calving, the index of fertility chosen by AGBU (Schneeberger *et al.*, 1991) may be inappropriate for tropical environments. The very low rates of pregnancy in some years (Table 5) ensures that a large proportion of cows (i.e. the non-pregnant cows) were allocated a "days to calving" value, which must reduce the normality of the distribution of the variable. The yearly variation in pregnancy rate (Table 5) and the importance of calf survival to weaning (Entwistle, 1983) would suggest that the search for an appropriate variable for the genetic improvement of female reproduction in the tropics should continue. Problems with the normal distribution of "days to calving", from a *Bos taurus* crossbred herd in temperate Australia, has lead Ponzoni and Gifford (1994) to conclude that the search for an appropriate variable for fertility for temperate Australia should also continue. For a detailed discussion of calving rate versus "days to calving", as the more suitable variable for fertility, see Ponzoni (1992).

4.2 Fixed effects

In the present study, once appropriate dependent variables were chosen, fixed effects were then identified. The fixed effects used to describe growth

(BWT, WWT, YWT and FWT) were environmental category, genotype, AGEPLS and sex of calf. Apart from sex of calf, which was non-significant, the same fixed effects were also used to describe pregnancy rate.

4.2.1 Environmental category

For both growth and fertility, using categories as a fixed effect, rather than years, enabled the variability between years to be grouped into different types of environment. Environmental categories have been used previously to address high variability between years in datasets of either growth or fertility (Vernon *et al.*, 1964; Frisch *et al.*, 1987; Itulya *et al.*, 1987; De Nise *et al.*, 1988; De Nise and Torabi, 1989).

Growth and Fertility

During the period over which the present study on "Belmont" extended, twelve calf crops changed their environmental category between birth and final weighing (see Tables 1, 2, 3 and 4) indicating the high degree of environmental variability on "Belmont". An example of the variability in environmental conditions on "Belmont" is seen in the 1983 calf crop. This crop of calves was born and weaned during the 1982/83 drought and consequently the BWT and WWT are in the poor years category (Tables 1 and 2). However, the YWT and FWT were in the good year category (Tables 3 and 4) which occurred because of a break in the drought conditions in 1983.

As with the growth parameters, the yearly pregnancy rates were also allocated into environmental categories that characterised the variation in pregnancy rates on "Belmont" (Table 5). Although three rather than two categories were used to balance the number of years and number of records in each category, the use of three categories did also identify extreme differences between good and poor years for pregnancy rate. The good years category was equivalent to the fertility normally expected of a benign temperate environment

(Reid, 1990) and the poor years were typical of a highly stressful tropical environment (Galina and Arthur, 1990b; Schlink *et al.*, 1994).

The implications of the high degree of environmental variability relate to the accuracy of genetic parameters and EBV's. De Nise *et al.* (1988, p.1899) note that "...manifestations of the environmental effects on estimations of breeding values are poorly defined and probably quite variable". Using good and poor environmental categories for a semi-arid environment, De Nise *et al.* (1988) and De Nise and Torabi (1989) have found that genetic parameters for growth change in response to the level of environmental stress. Frisch and Vercoe (1982, p.312) point out that "...an estimate of h^2 of growth rate measured in the presence of high levels of environmental stress is likely to be an estimate of the h^2 of resistance to those stresses. Conversely, in the absence of environmental stresses h^2 of W/A (weight per day of age) is an estimate of h^2 of growth potential". Thus, in a dry tropical environment the variability between years may also have a corresponding variability in the estimates of the genetic parameters for growth.

This issue of the relationship between the estimation of genetic parameters and environmental variability could be addressed by utilising data from the "Belmont" database. An estimation of the genetic parameters and EBV's for growth could be undertaken by firstly undertaking an analysis that ignored environmental categories, and secondly, repeating the analysis but within good and poor years categories. Of particular interest would be the ranking of sires for the performance of growth in the good versus poor years, where a sire has been used for more than one year. Thirdly, as the database also contains information on each sire's resistance to environmental stress (e.g. resistance to cattle tick and helminths), the correlations between the ranking of the sires for growth in the good versus poor years and their rankings for resistance to environmental stress could be investigated.

Indices for fertility

For the fertility dataset, years were assigned to an environmental category based on the pregnancy rate of that year and the same categories were used in the analysis of IWT and MWGD (Table 5). In this way IWT and MWGD were able to be observed in years in which the pregnancy rate was either good, average or poor. The two variables IWT and MWGD have been recognised as important indices of a cow's nutritional status and hence her reproductive status in tropical environments (Richardson *et al.*, 1975; Buck *et al.*, 1976; Entwistle, 1984; Frisch *et al.*, 1987; Anderson *et al.*, 1988). The grouping of years into three categories based on overall pregnancy rate is reflected in the IWT values, the heaviest IWT are in the good years and the lowest in the poor years (Table 5). The importance of IWT is further indicated by the positive regressions of pregnancy rate on IWT for 3 year old maidens (Table 10) and for lactating cows (Table 11). Although the regression of pregnancy rate on MWGD is also positive for cows 4 years of age and older (Tables 11 and 13), pregnancy rate is not reflected in MWGD. The highest levels of MWGD occur in the poor years and the lowest levels of MWGD occur in the good years (Tables 5 and 12). It is conceivable that in the good years for fertility, the cow's heavy body weight (IWT) leaves little capacity for high weight gain during the breeding season. Overall, these data support the conclusion of Richardson *et al.* (1975) and Steenkamp *et al.* (1975) that the best indicator of a cow's ability to rebreed is her liveweight at the start of the breeding season. Hence, this is evidence that a cow's long term nutritional status (IWT) is more important than her short term nutritional status (MWGD). This implies that further research into those management procedures, such as supplementary feeding and early weaning is warranted because the improved nutritional status of a lactating cow may (Tuen *et al.*, 1982; Loxton *et al.*, 1983; Ghosh *et al.*, 1993; McSweeney *et al.*, 1993) or may not (Holroyd *et al.*, 1983,1988; Schlink *et al.*, 1994) be associated with increased reproductive rates.

4.2.2 Genotype

In previous studies of growth and fertility of cattle on "Belmont" (Seebeck, 1973; Frisch and Vercoe, 1984; Frisch *et al.*, 1987; Mackinnon *et al.*, 1989; Hetzel *et al.*, 1990; Mackinnon *et al.*, 1991), the genotypes always included in the study were HS, BX and Brahman. Whereas the HS and Brahman are opposite for production potential and resistance to environmental stress, the BX is intermediate for both of these traits. The present study included these same genotypes for the same reasons. Although "Belmont" Brahmans have always consisted of both high and low grade, no previous study has ever investigated the influence of Brahman content on productivity. Separating Brahmans into high and low grade categories has demonstrated that Brahmans of different content also have different patterns of growth and fertility. Previous studies from other locations in northern Australia (e.g. Fordyce *et al.*, 1989; Holroyd *et al.*, 1990a,b) have also found that Brahman content is an important consideration in the analysis of both growth and fertility of beef cattle.

Growth

The effects of genotype on the calf's day of birth, birth weight and age adjusted weights at weaning, 365 days and 550 days for HS, BX and Brahmans reported in previous studies (Frisch and Vercoe, 1984; Hetzel *et al.*, 1990; Burrow *et al.*, 1991) are confirmed with this study. In general, the HS are born earlier and heavier than the other genotypes but from then on have the lowest growth rates of any of the genotypes (Table 6). Previous reports have shown the Brahmans are born latest and lightest but after weaning have superior growth rates. At weaning the BX is usually the heaviest genotype but it is intermediate for the other three growth parameters. The various changes in rank have been explained in terms of the differences in growth potential and resistance to environmental stress between *Bos taurus*, *Bos indicus* and the *Bos taurus* x *Bos indicus* crossbred (see Frisch and Vercoe, 1981,1984).

However, Table 6 also shows that separating the Brahmans into two lines based on Brahman content identifies two distinct patterns of growth within the Brahmans. These differences can be explained in terms of growth potential and resistance to environmental stress. Although BL calves are born earlier than BH calves, the differences are not significant. The issue of gestation length is complicated because BL and BH calves can be born to either BL or BH dams. However, liveweights associated with the maternal environment (BWT or WWT) show that the BL are significantly heavier than BH, indicating that the growth potential of the BL is higher than that of the BH and similar to that of the BX. Because the post-weaning growth of the BL approaches that of the BH in the poor years, it can be concluded that the level of resistance to environmental stress of the BL also approaches that of the BH. By FWT, the difference between BL and BH has been largely removed and both lines are heavier (P=0.06) than BX (Table 6).

The superiority of the BL for performance in growth rate supports the use of this genotype in the industry herds of northern Australia. Beef producers in this region have generally stabilised their herds at between ½ and ⅞th Brahman content because herds of lower or higher Brahman content experience reduced growth rates in their calves (Lapworth *et al.*, 1976).

At present the proportion of Brahman purebreeding is not considered in genetic evaluation models of growth that are used in the across-herd Brahman GROUP BREEDPLAN analysis (Schneeberger *et al.*, 1991). In other studies of other breeds the proportion of purebreeding was found to be a significant component in the analysis of liveweight data. Studies of growth rates in which this effect has been shown to be significant include those of Molina *et al.* (1982) with Romosinuano from Costa Rica (latitude 10°N), Graser and Hammond (1985) with Simmentals from southern Australia and Lubritz *et al.* (1987) with Chianina from Louisiana (latitude 30°N). Another potential source of variation not taken into account, for the GROUP BREEDPLAN analyses, is the differences between the recently imported Indu-Brazil from Brazil and Brahmans bred in Australia. Anecdotal information indicates that the Indu-Brazil is a large framed, late maturing *Bos indicus* and is significantly different from Australian Brahmans. Although the Indu-Brazil only contributed a relatively small number of sires to the GROUP BREEDPLAN analysis of 1993 and 1994 (Anonymous, 1993,1994), the sire trait leaders, for all traits, were almost exclusively of Indu-Brazil origin. The evidence from studies of the proportion of pure breeding (e.g. Graser and Hammond, 1985) and from Table 6 suggests that not accounting for various proportions of Brahman breeding and various proportions of Indu-Brazil breeding would be ignoring important sources of variation in the analysis of growth rates for Brahman GROUP BREEDPLAN.

Fertility

Rankings of HS, BX and Brahman (combined BL and BH) for pregnancy rate (Table 7) are the same as found in recent studies of fertility on "Belmont" (Frisch *et al.*, 1987; Mackinnon *et al.*, 1989). As with the growth parameters (Table 6) separating Brahmans into high and low grade gave two distinctly different performance levels for fertility. The pregnancy rate of BL was similar to HS and both were substantially higher than the pregnancy rate of BH. The higher rates of reproduction of the BL over the BH thus supports the use of low grade Brahman herds in northern Australia. The relatively high pregnancy rate of BL (Table 7), coupled with the high growth rates of BL calves (Table 6), makes the BL a better productive option for northern Australia than either BX, HS or BH. Peacock *et al.* (1969) also found that low grade Brahmans (between ½ and ⅞th Brahman content), at Florida (latitude 20°N) had higher growth and weaning rates than either purebred Brahmans or purebred Shorthorns.

Some of the higher productivity of BL (Tables 6 and 7) could be explained by heterosis resulting from progeny of ¾ content being born to F_1 Brahman x HS dams. However, as only a small number of animals originated from F_1 dams, the influence of heterosis was considered to be minor. Nevertheless, the higher performance of BL over BH as seen at "Belmont" and at other locations in the tropics and subtropics warrants the separation of Brahmans into categories based on the proportion of Brahman breeding in genetic evaluation models. The above finding suggest that the method used by Graser and Hammond (1985) for the genetic evaluation of Simmentals, that differed in grade, should also be applied to Brahmans.

4.2.3 Age of dam and previous lactational status

In the dry tropical environment of northern Australia, both the age of the dam and her previous lactational status are factors that affect growth and fertility.

Growth

The highly significant and consistent effects of AGEPLS on CBDAY, BWT, WWT, YWT and FWT (Table 8), support the results of numerous earlier studies from the tropics in which both age of dam and previous lactational status affect both time of calving and calf growth rate to 18 months of age (Berruecos and Robinson, 1968; Thorpe *et al.*, 1981; Rudder *et al.*, 1982a; Frisch and Veroce, 1984; Hetzel *et al.*, 1990; Mackinnon *et al.*, 1991; Ahunu *et al.*, 1993; Fordyce *et al.*, 1993a). Therefore, production systems that retain non-pregnant cows in their breeding programs must include both maternal effects, as fixed effects to describe models of calf's time of birth, and growth rate to at least 18 months of age.

Fertility

As with the growth parameters, AGEPLS was a highly significant effect in the analysis of pregnancy rate (Table 9). The significantly higher reproductive rates of both 3 year old maidens and non-lactating cows, over lactating cows, confirms previous reports from tropical environments (Holroyd *et al.*, 1977; Frisch *et al.*, 1987; Anderson *et al.*, 1988; Fordyce *et al.*, 1989; Mackinnon *et al.*, 1989).

The significantly higher pregnancy rates of maidens and non-lactating cows compared to lactating cows demonstrates the effect of lactational anoestrus (Table 9). The alternating high and low pregnancy rate for 3, 4, 5, 6 and 7 year old cows is consistent with the high degree of post-partum anoestrus (low pregnancy rate) occurring after a high pregnancy rate (Table 9). Table 9 indicates that lactational anoestrus is greatest in growing cows (4 year olds) and is less important once cows have reached their mature size (7-9 year olds). This indicates that cows that have yet to reach maturity, partition available nutrients between milk production and their requirements for maintenance, growth and resumption of oestrus.

The relationships between pregnancy rate and IWT, MWGD and DAYOC are complex. The alternating high and low pregnancy rate occurs despite an increasing IWT and a constant MWGD. The alternating pregnancy rate is also inconsistent with DAYOC. In general, cows with early born calves have been shown to have higher pregnancy rates (Table 11). However, 4 year old cows, despite their early DAYOC, are most prone to lactational anoestrus and achieve the lowest pregnancy rate (Table 9). Furthermore, the significant reduction in pregnancy rate after the cows have reached 9 years of age is related to some ageing process. This ageing process seems unlikely to be related to poor dentition, as surmised by Holroyd (1977) and Anderson *et al.* (1988) because the aged cows on "Belmont" do not have the need to walk long distances for feed and water and this age class had the heaviest IWT, and similar MWGD and DAYOC to the other lactating cows. There is an indication that the 4 year old non-lactating cows (i.e. cows that didn't conceive as 3 year old maidens) are genetically sub-fertile, because factors such as IWT, MWGD and DAYOC do not explain the relatively low pregnancy rates of this group (Table 9). The unexpected drop in fertility of non-lactating 4 year old cows has also been reported by Mackinnon (1988).

Fertility of maidens in different genotypes

The differences in pregnancy rates between maidens of any genotype are small and non-significant (Table 10). Compared to the three *Bos indicus* derived genotypes, the HS show typical *Bos taurus* attributes by their earlier HBDAY (Table 10). The relatively low growth rate of *Bos taurus* heifers compared to *Bos indicus* heifers, reported in other studies in the tropics (Seifert, 1975; Burrow *et al.*, 1991) are also shown in this study by the low IWT's of HS heifers (Table 10). However, once the HS heifers have reached 26 months of age their growth rate during the breeding season (MWGD) are not different from the other genotypes.

Fertility of lactating cows in different genotypes

Unlike the small differences between the maidens of different genotypes, the differences for lactating cows were large and highly significant. The ranking of HS, BX and Brahman (Table 11) for fertility has been reported previously (Frisch *et al.*, 1987; Mackinnon *et al.*, 1989). As with the comparison between HS maidens and the maidens of other genotypes (Table 10), HS lactating cows have lower IWT but a similar MWGD to the lactating cows of the other genotypes (Table 11). Despite the lower IWT, the HS achieve the highest pregnancy rate. A more detailed discussion of the relationship between HS, BX and Brahman and IWT, MWGD and DAYOC can found in Frisch *et al.* (1987).

As the present study separated Brahmans into high and low grade, the discussion on genotype differences for lactating cow fertility will focus on the reproductive performance of BL and BH cows. Compared to Brahmans of high grade, Brahmans of low grade had higher pregnancy rates, IWT and MWGD as well as an earlier DAYOC (Table 11). Of particular interest was the large difference in MWGD as, unlike the other genotypes, lactating BH cows barely gained any weight during the breeding season. Hohenboken *et al.* (1971) and Richardson *et al.* (1977) have shown that changes in weight of lactating cows during early lactation are negatively related to milk yield. Hence, the small MWGD of the BH (Table 11) was not surprising given the reports of the relatively high levels of milk production of high grade Brahmans when compared to *Bos taurus* beef breeds (Hentges and Howes, 1963; Holmes *et al.*, 1968; Brown *et al.*, 1993c).

The allocation of years into environmental categories also highlighted the differences between maidens and non-lactating cows on one hand and lactating cows on the other. Unlike maidens and non-lactating cows, lactating cows displayed a large variation in pregnancy rate between good, average and poor years. A pregnancy rate of 75.8% in lactating cows in good years (Table 12) resembles the pregnancy rate that would be achieved in a temperate environment (Reid, 1990). The corresponding pregnancy rates in the poor years (Table 12) resembles the high stress environments of the tropics (Galina and Arthur, 1989b; Chenoweth, 1994).

Once lactating cows had reached a mean IWT of about 450 kg at the start of the breeding season on "Belmont", the cows will achieve high pregnancy rate (Table 12). These pregnancy rates were achieved even if the MWGD was low. Conversely, if the IWT was low (390 kg) it does not matter if the MWGD was relatively high (0.30 kg/day) since the pregnancy rates will still remain low. This was further evidence that the short-term nutritional status during the breeding season (MWGD) was of less importance than the long-term nutritional status (IWT) and confirmed work by Richardson *et al.* (1975), Steenkamp *et al.* (1975) from Africa and Anderson *et al.* (1988) from northern Australia.

Fertility of non-lactating cows in different genotypes

Separating the Brahmans into high and low grade identified two distinct patterns for pregnancy rate, IWT and MWGD for non-lactating cows (Table 13). Apart from MWGD, which was relatively high and not different between the two lines, the pregnancy rate and IWT was again in favour of BL. Indeed the pregnancy rate of BL was not different from either HS or BX.

4.2.4 Sex of calf

Growth

Male calves were born later and had superior growth rates, especially at older ages, than female calves (Table 14). This pattern has been reported in numerous other studies from both tropical and temperate regions (Bair *et al.*, 1972; Barlow and O'Neill; 1978; Pell and Thayne, 1978; Fordyce *et al.*, 1993a).

Fertility

Preliminary analysis of the effect of sex of calf on fertility found no significant effect, as was found in other studies (Warnick *et al.*, 1967; Aaron *et al.*, 1990; Aaron and Thrift, 1990).

4.3 Interactions

In the present analysis, the four genotypes provided a range in Brahman content from zero (HS) to purebred (BH) and this enabled the investigation of interactions between genotype and the other fixed effects. The significant interactions between genotype and environmental category, maternal environment and sex of calf are discussed in detail. The occurrence of the interactions has implications for genetic improvement programs for this region.

4.3.1 Interaction between genotype and environmental category

A number of studies and reviews have been concerned with both the growth and reproductive performance of different genotypes in different environments (e.g. Bolton *et al.*, 1987a; Setshawaelo, 1990; Morris *et al.*, 1993) and how to handle these interactions in genetic evaluation procedures (e.g. Notter, 1991; Cameron, 1993).

Growth and Fertility

Grouping years into environmental categories enabled the investigation of the sensitivity of the genotypes to the different environmental categories. Vernon *et al.* (1964), Frisch *et al.* (1987) and Itulya *et al.* (1987) used similar environmental categories to investigate an interaction between genotype and environment. For the same reason, Frisch and Vercoe (1984) artificially imposed three different levels of environmental stress onto a single calf crop of HS, BX and Brahman on "Belmont" by using the following three treatments: pasture fed with no control of parasites (high stress environment); pasture fed and control of ticks and worms (medium stress environment); housed and fed lucerne *ad libitum* (low stress environment).

The findings of the present study (Figures 1 to 7) are essentially in agreement with the findings of Frisch and Vercoe (1984) and Frisch *et al.* (1987). In essence, the genotype of highest production potential and lowest level of resistance to environmental stress (HS) performs relatively better in the better environment and relatively poorly in the poor environment. The genotype of intermediate production potential and level of adaptation (BX) has an intermediate performance in both categories of environment. If the growth and reproductive rates of BL and BH were averaged, the average performance of the combined lines would be similar to the Brahmans in the two previous studies on "Belmont". The Brahmans, despite their low growth potential, achieved the highest growth rates in the high stress environment because of their high degree of resistance to environmental stress (Frisch and Vercoe, 1984). In years of high environmental stress the Brahmans had similar calf crops to the HS (selected line) and BX but were significantly below the HS and BX in the years of low environmental stress (Frisch *et al.*, 1987).

However, dividing Brahmans into high and low grade revealed that the two lines had different levels of production potential but similar levels of resistance to environmental stress. In the good years, the BWT of the BL is the same as that of the BX and significantly heavier than that of the BH (Figure 1), which provides evidence that the potential for growth of the BL is closer to that of the BX than of the BH. That reproduction potential of the BL is also closer to the BX than BH is indicated in Figure 5. For average and good years, the BX and BL had similar and significantly higher pregnancy rates than BH. Hence the data indicate that the production potential of the BL is similar to that of the BX and higher than that of the BH.

The growth performance of the BL compared to BH in the poor years provided an indication that the level of resistance of both genotypes is similar. The WWT, YWT and FWT of BL calves in the poor years were consistently heavier than the BH (Figures 2, 3 and 4 respectively). Similarly, in terms of fertility the BL achieved the higher pregnancy rate than BH in the poor years (Figure 5). In addition, the BL has both higher IWT (Figure 6) and MWGD (Figure 7) than the BH but the difference is greatest in the poor years. The higher IWT and MWGD of the BL would contribute to the higher pregnancy rate of this genotype, especially in the poor years.

A distinctive feature of the BL is that for both the post-calving weights of calves (Figures 2, 3 and 4) and pregnancy rates (Figure 5) there is very little variation between good and poor years. Hence, the relatively high productivity of low grade Brahmans discussed earlier is confirmed by the consistency of performance over a range of environmental conditions. Because of their relatively high levels of resistance to environmental stress the BL is able to realise a high proportion of its production potential, which is greater than that of the BH. However, a contributing factor to this high level of consistency could be heterosis in those ¾th Brahmans born to F_1 Brahman x HS cows which consisted of about 10% of the herd.

4.3.2 Interaction between genotype and maternal environment

Growth and Fertility

The interaction between genotype and maternal environment (AGEPLS) is significant for both WWT (Figure 8) and pregnancy rate (Figure 9) and, as also noted by Franke and Oviedo (1992), the variation in the effect of genotype is primarily related to the proportion of Brahman. However, the AGEPLS effects on WWT are opposite to the effects on pregnancy rate.

The AGEPLS effects are significantly higher in the HS than in the two Brahman lines and intermediate in the BX (Figure 8). This confirms studies that have shown age-of-dam effects for growth rates of calves to be less in *Bos indicus* derived breeds than in *Bos taurus* breeds (Seifert, 1975; Brown *et al.*, 1993a,b).

Conversely, for pregnancy rate, the AGEPLS effect for HS was minor compared to the effects in the Brahman derived genotypes (Figure 9). This has also been shown by Mackinnon (1988). However, not shown previously has been the differences in the AGEPLS effect between low and high grade Brahmans. Although all classes of AGEPLS for BH were lower than for BL, those BH cows that were 4 years of age and lactating were particularly prone to low reproductive rates. That factors other than IWT and MWGD are associated with this low pregnancy rate is indicated by the relatively high IWT and MWGD of BH cows (Figure 9). Despite the 4 year old lactating BH cows being 35 kg heavier and having no difference in MWGD to the comparable HS cows, the pregnancy rate of BH cows was 25.4% compared to 71.4% for the HS cows.

4.3.3 Interaction between AGEPLS and environmental category

Growth and Fertility

In the environment on "Belmont" the combination of age of dam and previous lactational status has been shown to be a significant fixed effect for all growth parameters (Table 8). When the overall means for all lines, in all years, are considered, the effects of the maternal environment on growth are reduced as the calf ages (Table 8). Similar findings have been reported for previous studies in the tropics (e.g. Seifert, 1975). Figure 10 shows that on "Belmont" whether or not the effects of the maternal environment have largely disappeared by 550 days of age depends upon the type of year. In the good years, correcting FWT for maternal effects would not be necessary. However, in the poor years, not adjusting FWT for the effects of AGEPLS would be ignoring significantly higher levels of environmental variation. If the FWT in poor years is not corrected for AGEPLS up to 18 kg differences between the classes of AGEPLS will be incorrectly taken as a genetic difference.

As with the growth parameters, the effects of the maternal environment on pregnancy rate also varies with environment conditions (Figure 11). This figure illustrates that the effects of lactational anoestrus are most pronounced in poor years. Compared to maidens and 5+ year old non-lactating cows, the 4 year old lactating cows also declined in pregnancy rate in the poor years but this decline was not related to either their IWT (Figure 12) or MWGD (Figure 13) in poor years. The decline in pregnancy rate occurred despite a relatively high IWT of 390 kg and a MWGD of 0.4 kg/day.

Rollins and Wagon (1956), Meyer (1992) and Waldron *et al.* (1993) have shown that ignoring maternal effects can significantly inflate the estimate of h^2 for preweaning growth traits. It follows that ignoring significant maternal effects on either post-weaning growth traits or reproductive traits would also distort the estimate of h^2 for these traits. This suggests that using either a standard set of adjustment factors or not adjusting for the interaction between AGEPLS and environmental category would be inadequate for models of genetic evaluation of productivity in this environment.

4.3.4 Interaction between genotype and sex of calf

Growth

It is well documented that male calves have higher growth rates than female calves but in environmentally stressful conditions the difference in growth rates between males and females may be either small or reversed (Frisch, 1981; De Nise *et al.*, 1988). Males are more affected than females because males are less resistant to environmental stress than females (Frisch, 1981) and this lower resistance is related to testosterone (Frisch and Hunter, 1990a,b). Compared to males of the Brahman derived genotypes, HS males have lower levels of resistance and higher levels of testosterone (Frisch and Hunter, 1990b) and therefore the difference between male and female in the HS is small compared to the corresponding difference in the Brahman derived genotypes (Figure 14). This suggests that in the dry tropics, there should be a simultaneous adjustment of growth rates for sex of calf and genotype. This was also a conclusion of Franke and Oviedo (1992) from their studies of growth rates of calves in the sub-tropics.

4.4 Covariates

The independent variables associated with time of calving (CBDAY, HBDAY and DAYOC) were found to describe a cause-and-effect relationship with productivity. Additionally, the independent variables, IWT and MWGD, were significantly related to fertility.

4.4.1 Time of birth

The day on which a cow calves has a simultaneous effect on the growth rate of that calf and the cow's subsequent fertility.

Growth

The onset of the wet season normally occurs about the middle of the calving period and hence the early born calves are usually born in the dry season and the late born calves are usually born in the wet season. The change from the unfavourable dry season to more favourable wet season environment is responsible for the positive regressions of CBDAY on both BWT and WWT (Table 6). By weaning, the early born calves have had longer exposure to ecto- and endo-parasites than the late born calves. Furthermore, dams of the early born calves, calve and approach peak lactation during the dry season whereas dams of the late born calves calve and reach peak lactation after the wet season has commenced. All of these factors contribute to early born calves growing at a slower rate than late born calves.

Positive regressions of time of calving on calf growth rates to weaning have also been found by Rudder *et al.* (1975), Seifert (1975), Newman and Deland (1991) and Fordyce *et al.* (1993a,b). Negative regressions (i.e. early born calves heavier than late born calves) would have agreed with the findings of Lesmeister *et al.* (1973), Seifert *et al.* (1974), Keller and Brinks (1978) and Rudder *et al.* (1982a). The implications for models of genetic evaluations are that time of birth is a significant covariate but whether the effect is positive or negative is specific for the production system.

Because a single time of weaning is used in the production system of "Belmont", calves born at the end of the calving period are weaned relatively early compared to calves born at the beginning of the calving period. The shorter nursing period of the late born calves is reflected in the negative regression coefficients of CBDAY on both YWT and FWT (Table 6). However, the regression coefficient is larger on YWT than on FWT (Table 6) and this indicates the CBDAY effect diminishes as the calf ages. Hence, 12 months after weaning, the effect of CBDAY still needs to be considered for models of growth in the tropics.

The change from positive (pre-weaning) to negative (post-weaning) relationships, shown in Table 6, have also been shown by Rege and Siboniso

(1993) for various genotypes of beef cattle in Zimbabwe (latitude 20°S).

Fertility

The time of birth of heifers also has implications for the parameters of fertility but the effect is not consistent between the genotypes. The within genotype regressions of the percentage pregnant on HBDAY can be grouped on Brahman content (Table 10). Whereas heifers of zero Brahman content (HS) are more fertile if they are born late, heifers of Brahman derivation are less fertile if they are born at the end of the calving period. These within genotype regressions have not been reported previously. The difference in the regression coefficients suggest that the heifers of some Brahman content have not reached puberty by the time of their first breeding season. Conversely, all HS heifers have reached puberty earlier, as shown by D'Occhio *et al.* (1994). However, the early born heifers consist of heifers born to non-lactating cows and the late born heifers were born to lactating cows (Table 8). This suggests that, unlike the three Brahman derived genotypes, non-lactating HS cows are genetically less fertile than their lactating contemporaries. Alternatively, the non-lactating HS cows are less adapted to a tropical environment than the lactating HS cows and the lower levels of resistance to environmental stress in these lactating cows is reflected in their lower reproductive rates in maidens. This further suggests that, unlike BX, BL and BH cows, retention of non-lactating HS cows in the breeding program, would be detrimental to the genetic improvement of the fertility of HS maidens. Culling non-lactating HS cows would remove those cows whose heifer progeny would have a reduced pregnancy rate as maidens. This would not be the case for the three Brahman derived genotypes. Furthermore, these differences suggest that there may also be corresponding differences in the genetic parameters for fertility between the HS and the BX, BL and BH.

The day of calving is also an important consideration for the genetic improvement of the fertility of lactating cows. The negative relationship between pregnancy rate and DAYOC shown in Table 11 agrees with numerous other studies in the tropics (Buck *et al.*, 1976; Holroyd, 1985; Frisch *et al.*, 1987; O'Rourke *et al.*, 1991a,b,1992). The negative regressions highlight the desirability of early calving in the tropics and suggest that genetic improvement programs should aim at reducing the DAYOC.

However, using EBV's for days to calving in order to increase the early calving rate of lactating cows may have little impact on the fertility of lactating Brahmans of high grade. The low reproductive rates of this genotype (Table 11), and especially of 4 year old cows (Figure 9), coupled with the exceptionally low MWGD of these cows (Table 11), would suggest that most cows of this genotype will only rebreed when their calves are weaned. Hence, early weaning is commonly employed as a means of increasing reproductive rate (Laster *et al.*, 1973a; Schlink *et al.*, 1988; Lusby *et al.*, 1991). It is hypothesised that the small proportion of BH cows that do rebreed without the calf being weaned would have a similar IWT and MWGD to the BX and BL and this warrants further investigation. Using EBV's for days to calving for BH cows is likely to be successful at reducing the days to calving in the small proportion of cows that rebreed but this procedure will be much less successful in the cows that exhibit lactational anoestrus. Hence EBV's for days to calving is not likely to significantly increase the reproductive rate of BH cows because of the high degree of lactational anoestrus in this genotype.

However, genetic improvement programs for BH cows that also aim at a target mating weight of around 430 kg and a MWGD of about 0.2 kg/day should, at least, increase the pregnancy rate of BH cows compared to that of BX and BL cows. This approach is likely to be successful, providing that the sucking stimulus, known to influence post-partum anoestrus (Wettemann *et al.*, 1978; Carruthers *et al.*, 1980; Bluntzer *et al.*, 1989) is the same between BX, BL and

BH cows. The author could find no evidence in the literature that the negative effects of the sucking stimulus are stronger in high grade Brahmans compared to low grade Brahmans. The evidence from the present study adds to the concerns of Davis (1993) and Frisch (1993) that the genetic improvement of reproduction, and especially of high grade Brahmans, will come from sources other than EBV's for days to calving.

4.4.2 Indices for fertility

Body condition score, cow liveweight going into the breeding season, and change in weight during the breeding season, have been shown to be useful indices for fertility in the tropics (Doogan *et al.*, 1991; De Rouen *et al.*, 1994 and see review by Randel, 1990). Although condition scores were not measured on the cows in the present study, in general, IWT and MWGD were shown to be significant covariates with pregnancy rate (Tables 10, 11 and 13). The relationship between these two indices and pregnancy rate was always positive, agreeing with numerous other studies in the tropics (Richardson *et al.*, 1975; Buck *et al.*, 1976; Goddard *et al.*, 1980; Frisch *et al.*, 1987; Mackinnon *et al.*, 1989; MacGregor and Swanepoel, 1992). However, IWT and MWGD must be looked at separately because these two indices do not necessarily have positive effects simultaneously. For instance, statistically adjusting pregnancy rate of HS lactating cows for their high MWGD would reduce pregnancy rate of HS lactating cows but because this genotype has the lowest IWT, adjusting for IWT then increases pregnancy rate (Table 11).

Genetically increasing the IWT of maidens, by selecting for high growth rate in the presence of environmental stress, will generally increase their pregnancy rates (Table 10). However, the relationship between pregnancy rate and IWT is stronger in BH maidens than in other maidens and this suggests that increasing the target IWT of BH maidens above 326 kg will increase their pregnancy rates more so than increasing the IWT of the other genotypes. Increasing the target weight of *Bos indicus* heifers, to increase reproductive rates, was also one of the key recommendations of Chenoweth (1994) in his review of reproduction in female *Bos indicus* cattle.

Use of environmental categories has shown that the relationship between pregnancy rate and IWT is not consistent for all environmental conditions (Table 11). The relatively small effect of changes in IWT in good years is because of the relatively high IWT in those years (Table 12). Conversely in poor years increasing the IWT of lactating cows has a greater influence on pregnancy rate. Thus selection for increased levels of resistance, would effectively increase IWT and therefore, pregnancy rate in the poor years.

In both lactating and non-lactating cows MWGD was a highly significant covariate for pregnancy rate (Tables 11 and 12). The response in pregnancy rate from an increase in MWGD would be small but nevertheless this is still a genetic improvement option that could be pursued.

4.5 Conclusions

Artificially improving the environment of northern Australia is one means by which an increase in the productivity of beef cattle can be achieved. An alternative is to develop a genotype that is highly productive in this region. One strategy that can be used to develop such a genotype is to select replacement breeding stock based on EBV's. However, as discussed in Chapter 1, a successful application of the mixed model technology can only be achieved if the models used to generate EBV's are an accurate reflection of both the production system and environment. There is ample evidence in the literature that models of growth and fertility of *Bos taurus* in a temperate environment are not transferable to *Bos indicus* in a tropical environment.

The survey of the literature acknowledges a large body of evidence of the factors that should be considered in the construction of models of growth and fertility. However, nominating these factors as components of genetic evaluation models is not straight forward in the tropics. Problems arise for the following three reasons;

i. The variables of growth and fertility, chosen for genetic improvement, do not always identify those traits that will maximise genetic gain in on-farm productivity;

ii. There is a lack of clear and unambiguous definition of both genotype and environment;

iii. The variability between years and between seasons is such that there is a lack of consistency within the components of models of growth and fertility.

The traits chosen for genetic improvement should match both the production system and environment of the region. This thesis presents a case for the production systems of northern Australia. For these late-weaning systems, traits for growth that should be targeted are birth weight and a 200 day weaning weight, a 365 day yearling weight and a 550 day weight. Traits for fertility, in such a system, should be traits such as pregnancy rate, calving rate or calf crop and not days to calving. However, if the system is based on early weaning then a 100 day weaning weight should replace the 200 day weight and days to calving could be considered as a trait for fertility.

Having identified the appropriate dependent variables, the next step in the construction of a model is to nominate the appropriate fixed effects, interactions and covariates. It has now been established that the improvement of an animal's productivity in a specific environment, requires the genetic improvement of those traits determining productivity in that environment, and not some other environment (see Falconer, 1989). However, in the dry tropics, beef cattle can be subjected to good and poor environmental conditions, not only between years, but also within a year. Environmental categories (see section 3.1.1) clearly defined the yearly variation in the growth and fertility data. Similarly, weighing calves at the ages of 365 and 550 days coincided with growth rates at the end of the normal dry and wet seasons respectively. Hence, environmental categories and weighing ages at 365 and 550 days were able to define the environmental conditions of this region.

The frequency and severity of poor years, and the low growth rates of calves to their yearling weight, designates that the genotypes used in this region must possess relatively high levels of resistance to environmental stress. For this reason the cattle used in this region are of varying Brahman content. However, the genetic evaluation models currently used in the tropics ignore Brahman content as a main effect. The recent infusion of other *Bos indicus* breeds (e.g. Indu-Brazil) into the northern herd, likewise has been ignored. That the genotype of the northern herd can be defined on Brahman content (BX, BL and BH) is demonstrated in section 3.1.2. Defining genotype in this way enabled the investigation of the relationship of Brahman content with the other fixed effects and covariates. These data suggest that the inclusion of Brahman content would provide a clear and unambiguous definition of genotype for models of genetic evaluation.

In northern Australia, the low reproductive rates in general, and the presence of high grade Brahmans in particular, has meant that a significant proportion of herds can consist of cows that were non-lactating in the previous breeding season. However, models currently being used for genetic evaluation of both growth and fertility ignore the effect of previous lactational status and use only age of dam as a main effect. Whereas only age of dam is applicable for temperate environments, section 3.1.3, provides evidence that both age of dam and previous lactational status should be considered for models that are to be used in the tropics. Moreover, age of dam/previous lactational status has a significant effect on post-weaning growth rates but by 18 months of age the effect is only significant in those years defined as poor.

The large number of significant interactions (Figures 1 to 14) and the significant covariates (Tables 6, 10, 11 and 13) indicates that there is a high degree of complexity in the biology of beef production in this environment. However, within this complexity there was a consistent pattern in the growth and fertility data that was explained by factors such as environmental category, level of *Bos indicus* content, maternal environment, day of calving, sex of calf and the indices of fertility, IWT and MWGD. These data imply that the accuracy of EBV's for both growth and fertility will be seriously compromised if a simple model and/or a single set of correction factors were to be applied to all data emanating from tropical Australia. These data suggest that the model and correction factors should be specific for the production system (early versus late weaning), season (365 and 550 day weights), type of year (good versus poor), genotype (*Bos taurus* versus *Bos indicus* and within *Bos indicus*, high content versus low content), sex of calf and maternal environment (both age of dam and previous lactational status).

Once the appropriate fixed effect have been identified, the final step in the genetic evaluation procedure would be to include genetic terms (random effects) into the models. Genetic evaluation models that incorporate all of these factors are viewed as a means by which not only the accuracy of the predication of genetic merit, but also the take-up rate of the technology in northern Australia can be increased. Furthermore, genetic improvement programs for growth and fertility could also consider exploiting the benefits of heterosis and improving the level of productivity in the poor years and seasons by increasing the level of resistance to environmental stress. Beef producers who employ strategies that simultaneously improve the environment and the genetic performance of their cattle will ensure that their improvement in on-farm productivity is both substantial and sustainable.

TABLE 1. Allocation of calf crops (1974 to 1990) into an environmental category either above or below the overall mean BWT of 31.6 kg ("good" and "poor" years respectively) with least squares mean BWT (±SE_m) for each calf crop and environmental category.

Calf crop (year)	N	BWT (kg)	Environmental category	N	BWT (kg)
1978	112	33.7±0.44			
1980	160	32.5±0.37			
1982	231	32.3±0.31			
1983	194	31.8±0.34	Good	1483	32.4±0.12
1985	211	32.0±0.32			
1986	222	32.0±0.31			
1989	211	33.2±0.32			
1990	142	32.2±0.39			
1974	167	30.9±0.36			
1975	177	31.5±0.35			
1976	146	31.0±0.39			
1977	180	28.7±0.35	Poor	1464	30.7±0.12
1979	216	31.3±0.32			
1984	120	30.2±0.43			
1987	221	31.5±0.32			
1988	237	30.2±0.30			

TABLE 2. Allocation of calf crops (1974 to 1990) into an environmental category either above or below the overall mean WWT of 173.8 kg ("good" and "poor" years respectively) with the least squares mean WWT (±SE_m) for each calf crop and environmental category.

Calf crop (year)	N	WWT (kg)	Environmental category	N	WWT (kg)
1974	112	185.8±2.27			
1984	116	188.8±2.67			
1985	201	187.4±2.02	Good	1310	185.5±0.81
1986	192	179.6±2.07			
1987	209	183.9±1.98			
1988	229	184.5±1.90			
1989	204	190.1±2.01			
1975	164	158.8±2.24			
1976	121	149.5±2.61			
1977	166	172.7±2.23			
1978	51	167.0±4.02	Poor	1174	165.6±0.85
1979	62	157.3±3.64			
1980	152	172.6±2.33			
1982	219	168.6±1.94			
1983	97	162.4±2.91			
1990	142	172.0±2.41			

TABLE 3. Allocation of calf crops (1974 to 1990) into an environmental category either above or below the overall mean YWT of 193.5 kg ("good" and "poor" years respectively) with the least squares mean YWT ($\pm SE_m$) for each calf crop and environmental category.

Calf crop (year)	N	YWT (kg)	Environmental category	N	YWT (kg)
1974	91	199.6±3.10			
1975	89	196.2±3.13			
1978	57	197.4±3.92			
1983	80	200.1±3.30	Good	1126	200.1±0.90
1984	117	199.7±2.73			
1986	93	206.7±3.07			
1987	211	196.4±2.03			
1988	228	198.5±1.96			
1989	160	206.8±2.34			
1976	42	181.0±4.56			
1977	63	187.4±3.72			
1979	37	187.0±4.86			
1980	93	189.3±3.07	Poor	541	183.3±1.30
1982	139	165.7±2.51			
1985	26	190.2±5.80			
1990	141	193.4±2.50			

TABLE 4. Allocation of calf crops (1974 to 1990) into an environmental category either above or below the overall mean FWT of 283.5 kg ("good" and "poor" years respectively) with the least squares mean FWT (±SE_m) for each calf crop and environmental category.

Calf crop (year)	N	FWT (kg)	Environmental category	N	FWT (kg)
1974	79	293.2±4.89			
1976	38	298.7±7.05			
1983	78	308.7±4.92			
1984	115	284.0±4.05	Good	1043	295.0±1.37
1986	92	314.0±4.53			
1987	209	288.1±3.01			
1988	227	294.9±2.89			
1989	205	294.6±3.04			
1975	76	282.0±4.99			
1977	44	268.8±6.56			
1978	32	277.8±7.69			
1979	37	278.0±7.15	Poor	557	265.0±1.88
1980	89	256.5±4.61			
1982	135	255.8±3.74			
1985	25	283.1±8.70			
1990	119	258.4±3.99			

TABLE 5. Least squares mean (±SE_m) for pregnancy rate per year from 1974 to 1990 and the allocation of years into an environmental category of either "good", "average" or "poor" years for pregnancy rate with least squares means (±SE_m) pregnancy rate, IWT and MWGD for each environmental category.

Pregnancy rate per year			Environmental category				
Year	N	Pregnancy rate (%)	Category	N	Pregnancy rate (%)	IWT (kg)	MWGD (kg/day)
1974	428	78.0±2.10					
1984	274	81.0±2.62					
1985	197	78.2±3.10					
1987	308	80.5±2.48	Good	1856	81.0±1.10	434.1±1.40	0.22±0.011
1989	303	85.5±2.50					
1990	346	82.7±2.34					
1975	373	77.2±2.25					
1981	285	77.2±2.57					
1982	299	70.6±2.51	Average	1652	74.1±1.07	404.6±1.63	0.33±0.012
1986	334	72.7±2.38					
1988	361	72.6±2.29					
1976	377	62.6±2.24					
1977	250	56.4±2.75	Poor	1092	57.3±1.32	387.8±2.54	0.37±0.019
1980	261	52.9±2.69					
1983	204	54.4±3.04					

TABLE 6. Least squares mean values (±SE_m) for CBDAY, BWT, WWT, YWT and FWT of HS, BX, BL and BH calf crops from 1974 to 1990.

Line	CBDAY (days)	BWT (kg)	WWT (kg)	YWT (kg)	FWT (kg)
HS	31.1±0.61 (1073)[a]	32.6±0.15 (1073)	154.7±0.97 (886)	168.2±1.16 (576)	240.2±1.64 (533)
BX	37.6±0.59 (1194)	31.2±0.14 (1194)	188.0±0.98 (994)	203.3±1.07 (659)	298.7±1.50 (624)
BL	43.1±1.15 (263)	31.0±0.28 (263)	187.9±2.17 (231)	209.7±2.35 (166)	306.0±3.38 (170)
BH	43.3±0.92 (417)	29.2±0.22 (417)	183.7±1.61 (373)	205.9±1.78 (266)	304.6±2.43 (273)

Regression of CBDAY on BWT over all lines and both year categories: $\beta_1 = 0.034 \pm 0.004$
Regression of CBDAY on WWT over all lines and both year categories: $\beta_2 = 0.144 \pm 0.024$
Regression of CBDAY on YWT over all lines and both year categories: $\beta_3 = -0.218 \pm 0.031$
Regression of CBDAY on FWT over all lines and both year categories: $\beta_4 = -0.163 \pm 0.043$

[a] number of observations in parentheses

TABLE 7. Number of animals and least squares means ($\pm SE_m$) for pregnancy rate for HS, BX, BL and BH females from 1974 to 1990.

Line	N	Number of animals	Pregnancy rate (%)
HS	1682	618	74.5±1.34
BX	1750	678	69.0±1.20
BL	402	140	74.2±3.14
BH	766	279	58.8±1.87

TABLE 8. Least squares mean values (±SE_m) for CBDAY, BWT, WWT, YWT and FWT of calf crops within each class of AGEPLS over all lines from 1974 to 1990.

AGEPLS (year class)		CBDAY (days)	BWT (kg)	WWT (kg)	YWT (kg)	FWT (kg)
3	Maidens	35.3±0.71 (724)[a]	29.8±0.17 (724)	171.1±1.05 (633)	191.2±1.27 (436)	283.3±1.84 (422)
4	Lactating	45.8±1.13 (282)	30.6±0.27 (282)	178.2±2.32 (247)	199.5±1.90 (182)	283.2±2.82 (179)
5+	Lactating	43.9±0.60 (1090)	31.4±0.15 (1090)	182.2±0.93 (949)	199.9±1.13 (607)	289.4±1.60 (587)
4	Non-lactating	36.7±1.47 (155)	31.0±0.35 (155)	175.6±2.25 (121)	194.2±2.66 (84)	286.8±4.06 (79)
5+	Non-lactating	32.2±0.72 (696)	32.1±0.17 (696)	185.9±1.10 (534)	199.0±1.36 (358)	294.2±1.91 (333)

[a] number of observations in parentheses

TABLE 9. Least squares mean (± SE_m) for pregnancy rate, IWT, MWGD and DAYOC for each class of AGEPLS over all lines from 1974 to 1990.

AGEPLS (year class)		N	Pregnancy rate (%)	IWT (kg)	MWGD (kg/day)	DAYOC (days)
3	Maiden	1021	81.5 ± 1.62	332.9 ± 1.87	0.58 ± 0.014	-
4	Lactating	629	48.6 ± 2.33	369.8 ± 2.69	0.19 ± 0.020	35.1 ± 0.91
5	Lactating	437	66.8 ± 2.84	405.2 ± 3.28	0.17 ± 0.025	41.5 ± 1.01
6	Lactating	433	63.4 ± 2.59	428.9 ± 3.00	0.18 ± 0.026	37.4 ± 1.00
7-9	Lactating	811	69.8 ± 1.93	447.3 ± 2.23	0.19 ± 0.017	39.8 ± 0.97
10+	Lactating	289	60.2 ± 2.99	452.5 ± 3.45	0.17 ± 0.026	39.0 ± 1.17
4	Non-lactating	220	70.3 ± 3.58	398.9 ± 4.14	0.49 ± 0.031	-
5+	Non-lactating	760	80.7 ± 1.90	445.3 ± 2.20	0.52 ± 0.017	-

TABLE 10. Least squares means (±SE_m) for pregnancy rate of 3 year old HS, BX, BL and BH maidens both alone and adjusted simultaneously for differences in HBDAY and IWT, and least squares means (± SE_m) for HBDAY, IWT and MWGD.

Line	N	Pregnancy rate (%)	Adjusted pregnancy (%)	HBDAY (days)	IWT (kg)	MWGD (kg/day)
HS	388	83.0±1.92	86.5±2.41	31.4±1.00	292.2±1.95	0.60±0.012
BX	382	82.9±0.92	82.9±2.00	35.2±0.99	333.1±1.94	0.60±0.012
BL	111	79.2±3.59	78.2±4.75	38.2±2.03	342.2±3.64	0.57±0.026
BH	124	79.6±3.39	78.1±3.77	43.9±1.94	326.0±3.44	0.55±0.024

Within genotype regression of percentage pregnant on HBDAY over all environmental categories :

in HS	$\beta_1 = 0.24 \pm 0.013$
in BX	$\beta_2 = -0.04 \pm 0.110$
in BL	$\beta_3 = -0.32 \pm 0.181$
in BH	$\beta_4 = -0.10 \pm 0.133$

Within genotype regression of percentage pregnant on IWT over all environmental categories :

in HS	$\beta_5 = 0.09 \pm 0.050$
in BX	$\beta_6 = 0.00 \pm 0.046$
in BL	$\beta_7 = 0.11 \pm 0.105$
in BH	$\beta_8 = 0.27 \pm 0.008$

TABLE 11. Least squares means ($\pm SE_m$) for pregnancy rates of lactating HS, BX, BL and BH cows both alone and adjusted simultaneously for differences in IWT, MWGD and DAYOC, and the least squares means ($\pm SE_m$) for IWT, MWGD and DAYOC.

Line	N	Pregnancy rate (%)	Adjusted pregnancy (%)	IWT (kg)	MWGD (kg/day)	DAYOC (days)
HS	988	70.9±1.57	73.9±1.64	389.4±1.69	0.21±0.014	32.0±0.63
BX	1000	59.9±1.48	58.4±1.51	431.4±1.60	0.21±0.014	37.5±0.60
BL	208	61.1±3.31	60.4±3.31	437.9±4.69	0.26±0.040	40.9±1.76
BH	387	49.9±2.43	52.7±2.46	415.9±3.06	0.08±0.026	44.0±1.15

Regression of pregnancy rate on IWT:
in good years $\beta_1 = 0.08 \pm 0.024$
in average years $\beta_2 = 0.16 \pm 0.026$
in poor years $\beta_3 = 0.19 \pm 0.030$

Regression of pregnancy rate on MWGD:
over all years $\beta_4 = 8.69 \pm 2.157$

Regression of pregnancy rate on DAYOC:
over all years $\beta_5 = -0.17 \pm 0.047$

TABLE 12. Least squares means ($\pm SE_m$) for pregnancy rates, IWT and MWGD for lactating cows in each environmental category.

Environmental category	N	Pregnancy rate (%)	IWT (kg)	MWGD (kg/day)
Good	1055	75.8±1.51	449.1±1.78	0.06±0.015
Average	921	65.5±1.64	415.5±2.11	0.21±0.017
Poor	607	40.2±2.04	391.3±3.71	0.31±0.031

TABLE 13. Least squares means (±SE_m) for pregnancy rate of non-lactating HS, BX, BL and BH cows both alone and adjusted for MWGD, and least squares means for IWT and MWGD.

Line	N	Pregnancy rate (%)	Adjusted pregnancy (%)	IWT (kg)	MWGD (kg/day)
HS	301	77.2±2.45	76.1±2.46	394.3±3.36	0.60±0.019
BX	361	78.1±2.37	77.9±2.35	440.8±3.24	0.54±0.018
BL	79	75.6±4.74	77.3±4.74	440.5±6.50	0.41±0.037
BH	238	67.8±2.80	69.2±2.81	419.0±3.84	0.43±0.022

Regression of non-lactating cow pregnancy rate on MWGD over all years : β_1 = 14.8±4.07

TABLE 14. Least squares mean values (±SE_m) for CBDAY, BWT, WWT, YWT and FWT of male and female calf crops over all lines from 1974 to 1990.

Sex	CBDAY (days)	BWT (kg)	WWT (kg)	YWT (kg)	FWT (kg)
Male	39.8±0.58 (1514)[a]	32.3±0.15 (1514)	185.6±0.92 (1276)	204.2±1.21 (825)	299.2±1.68 (756)
Female	37.8±0.59 (1433)	29.7±0.15 (1433)	171.6±0.93 (1208)	189.3±1.15 (832)	275.5±1.57 (844)

a number of observations in parentheses

TABLE 15. The mean BWT of HS, BX and Brahman calves prior to 1974 compared to the correpsonding BWT's for the present study.

Line			Authors
HS	BX	Brahman	
33.2	29.8	-	Seifert and Kennedy, 1966
31.8	29.7	-	Kennedy and Chirchir, 1971
27.6	29.5	23.9	Frisch, 1973
31.9	-	-	Seebeck and Seebeck, 1982
-	-	27.8	Preston and Willis, 1974
32.6	31.2	30.1*	present study (Table 6)

* combined BL and BH lines

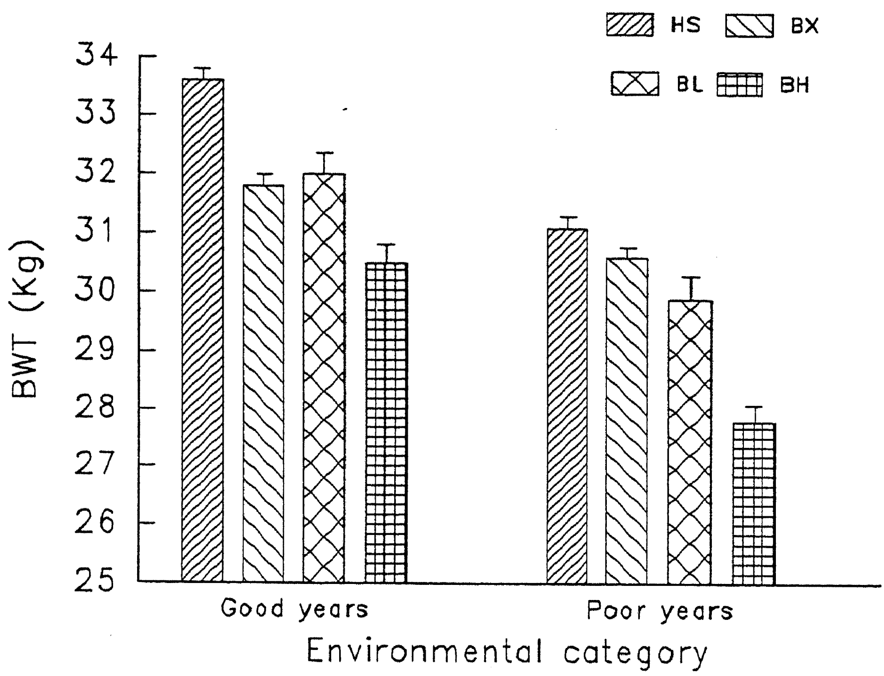

FIGURE 1

Interaction of genotype by environmental category for BWT of all calf crops from 1974 to 1990.

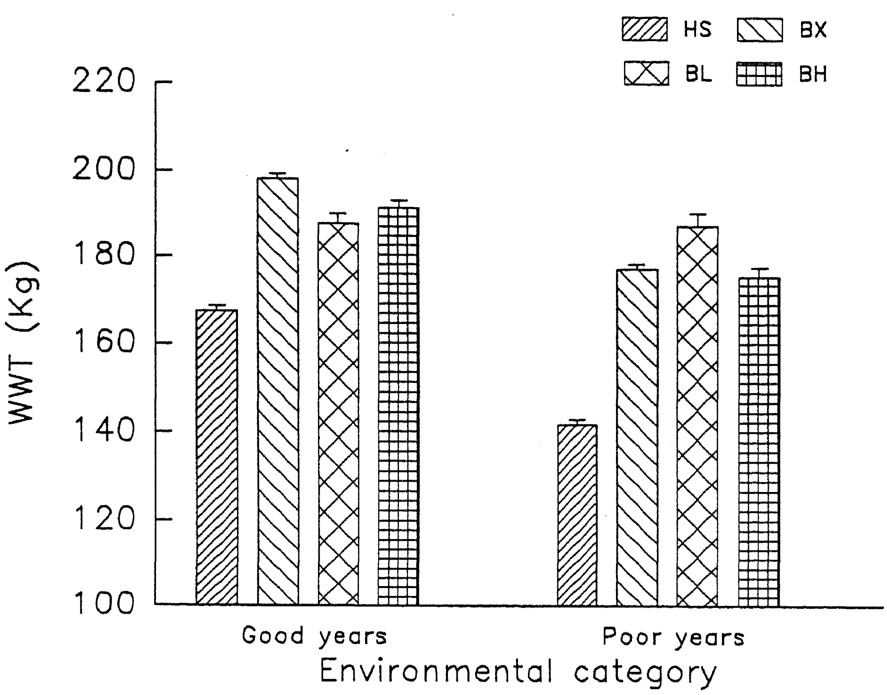

FIGURE 2

Interaction of genotype by environmental category for WWT of all calf crops from 1974 to 1990.

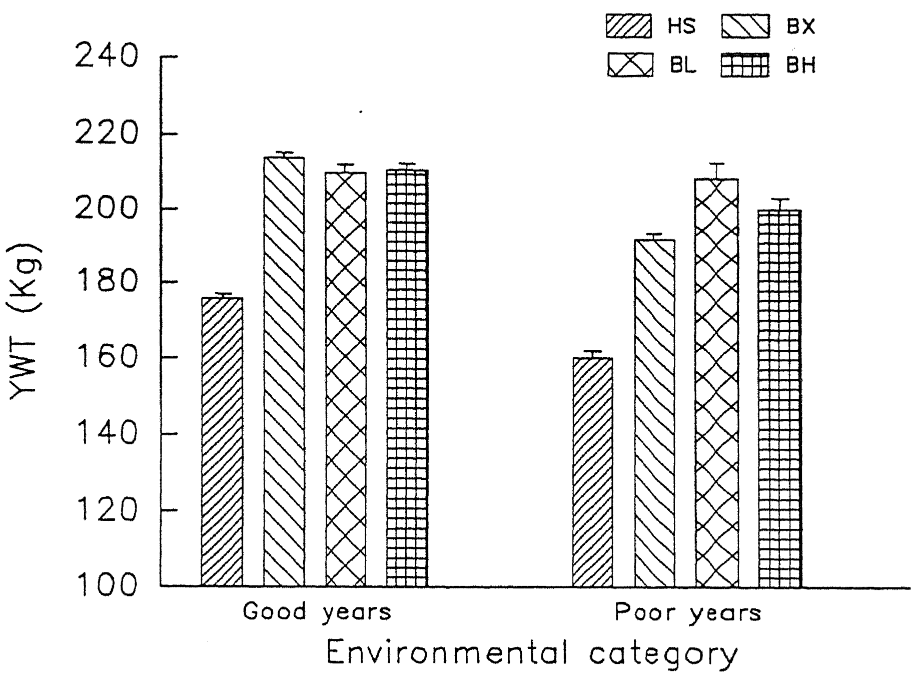

FIGURE 3

Interaction of genotype by environmental category for YWT of all calf crops from 1974 to 1990.

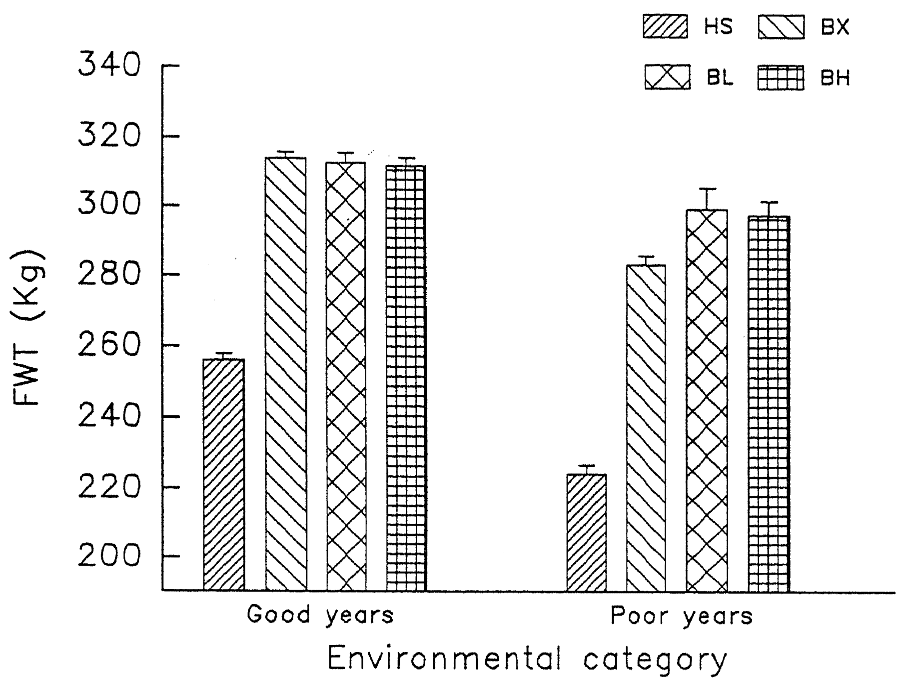

FIGURE 4

Interaction of genotype by environmental category for FWT of all calf crops from 1974 to 1990.

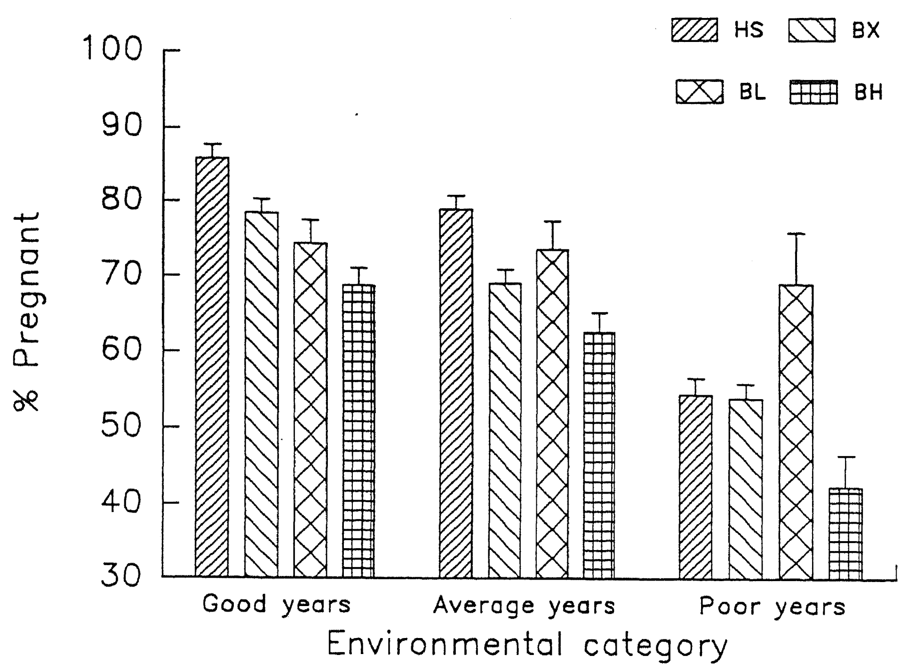

FIGURE 5

Interaction of genotype by environmental category for pregnancy rate of all classes of AGEPLS from 1974 to 1990.

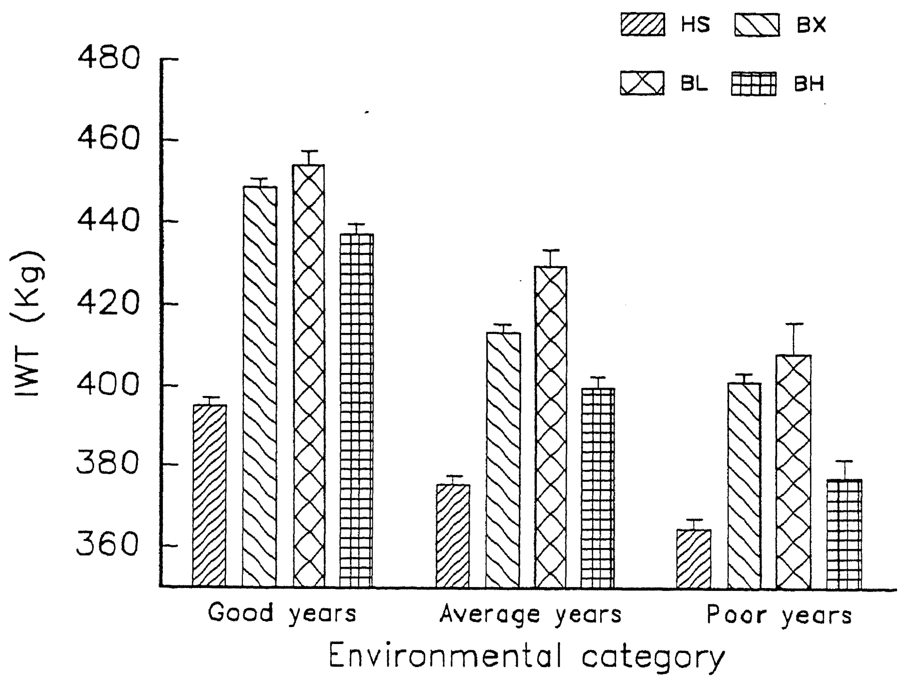

FIGURE 6

Interaction of genotype by environmental category for IWT of all classess of AGEPLS from 1974 to 1990.

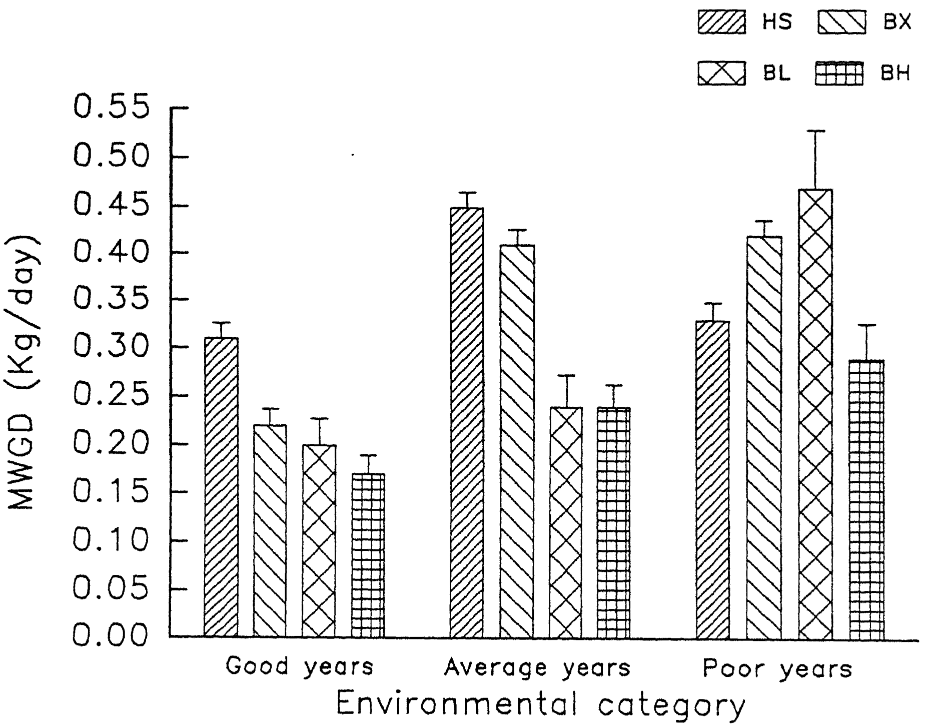

FIGURE 7

Interaction of genotype by environmental category for MWGD of all classes of AGEPLS from 1974 to 1990.

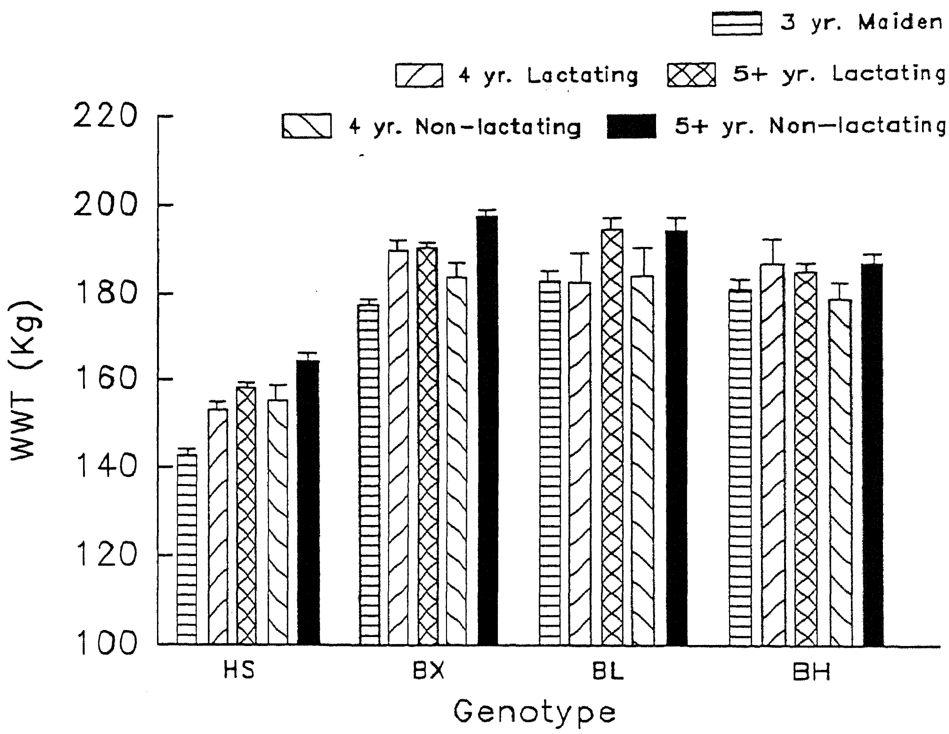

FIGURE 8

Interaction of AGEPLS by genotype for WWT of all calf crops from 1974 to 1990.

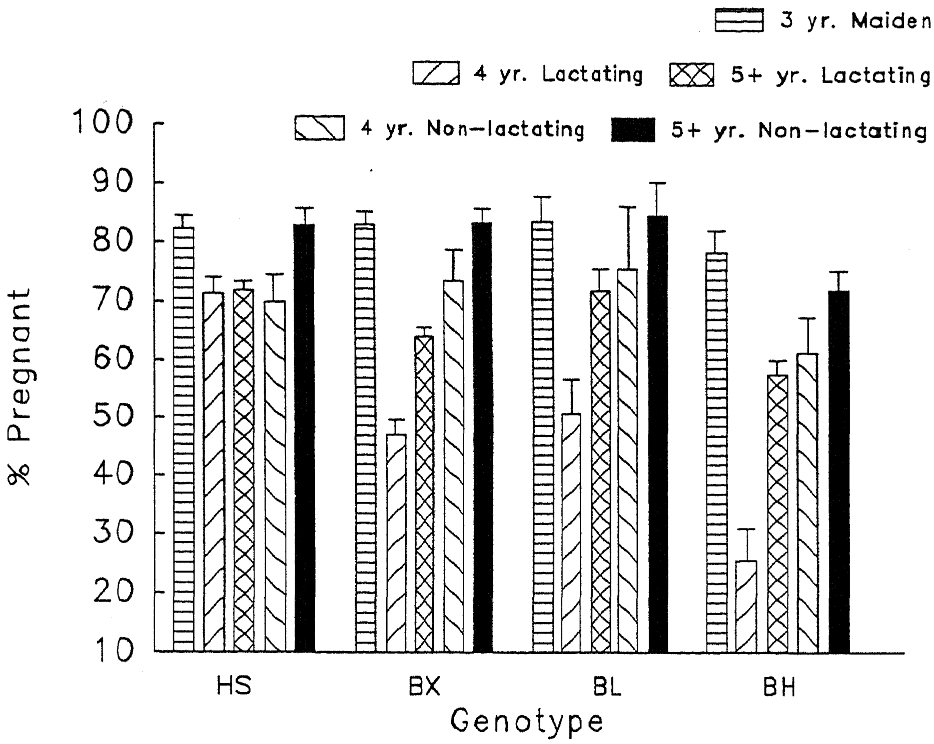

FIGURE 9

Interaction of AGEPLS by genotype for pregnancy rate from 1974 to 1990.

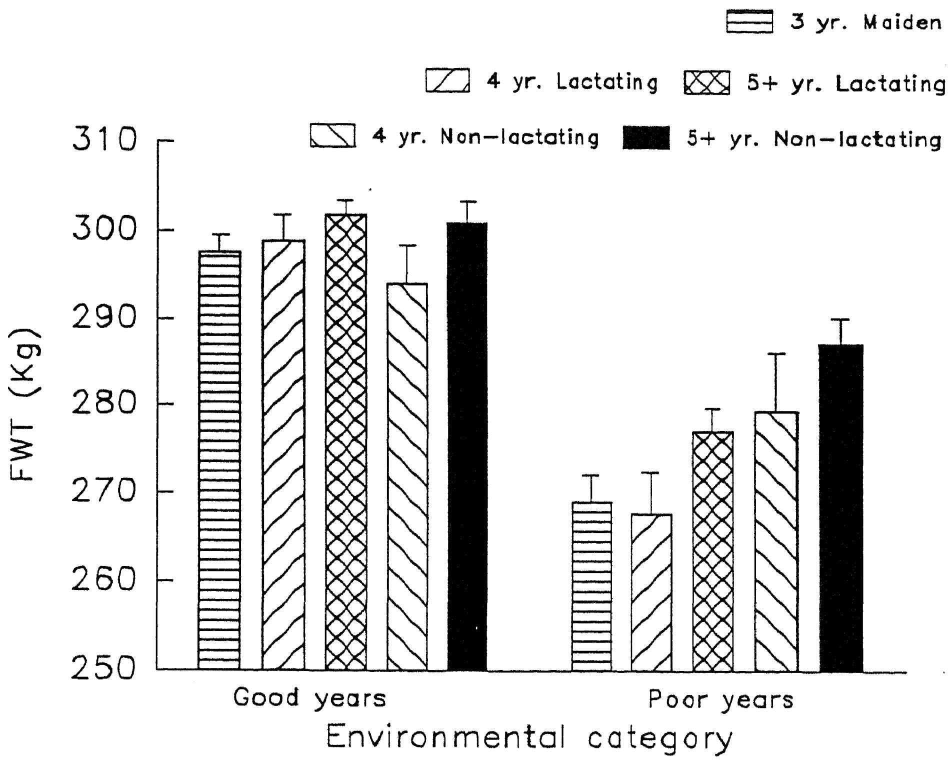

FIGURE 10

Interaction of AGEPLS by environmental category for FWT of all calf crops from 1974 to 1990.

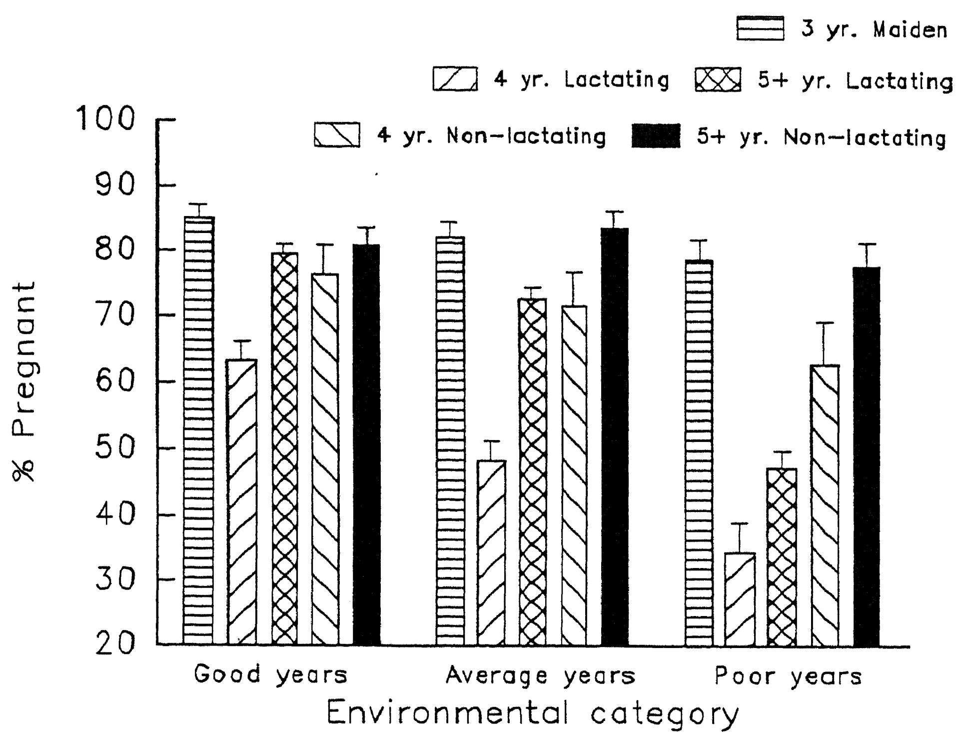

FIGURE 11

Interaction of AGEPLS by environmental category for pregnancy rate of all genotypes from 1974 to 1990.

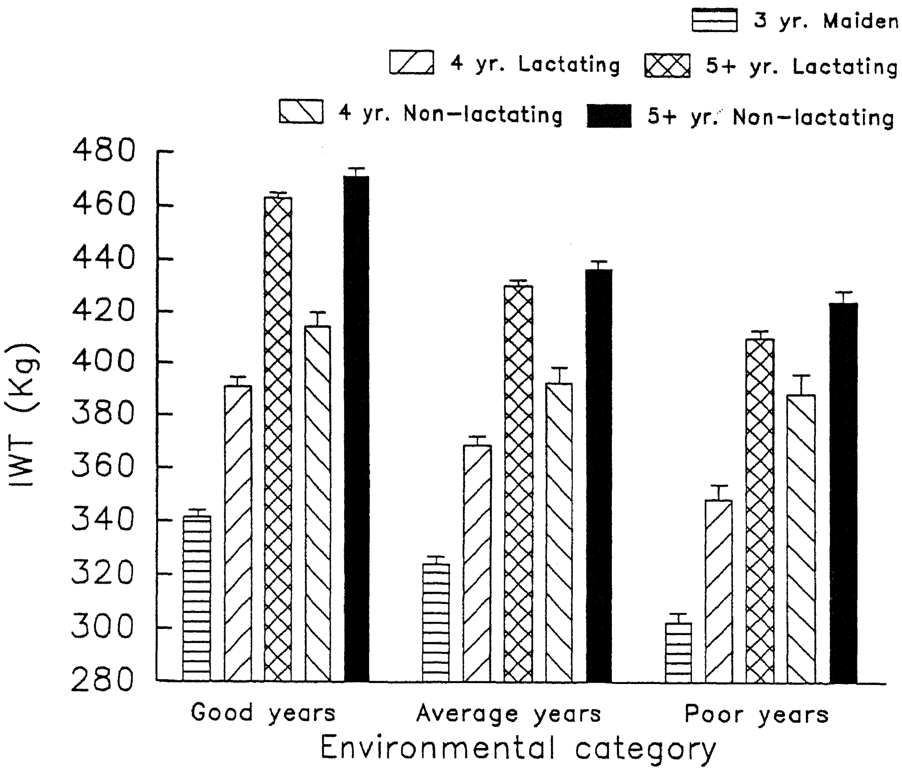

FIGURE 12
Interaction of AGEPLS by environmental category for IWT of all genotypes from 1974 to 1990.

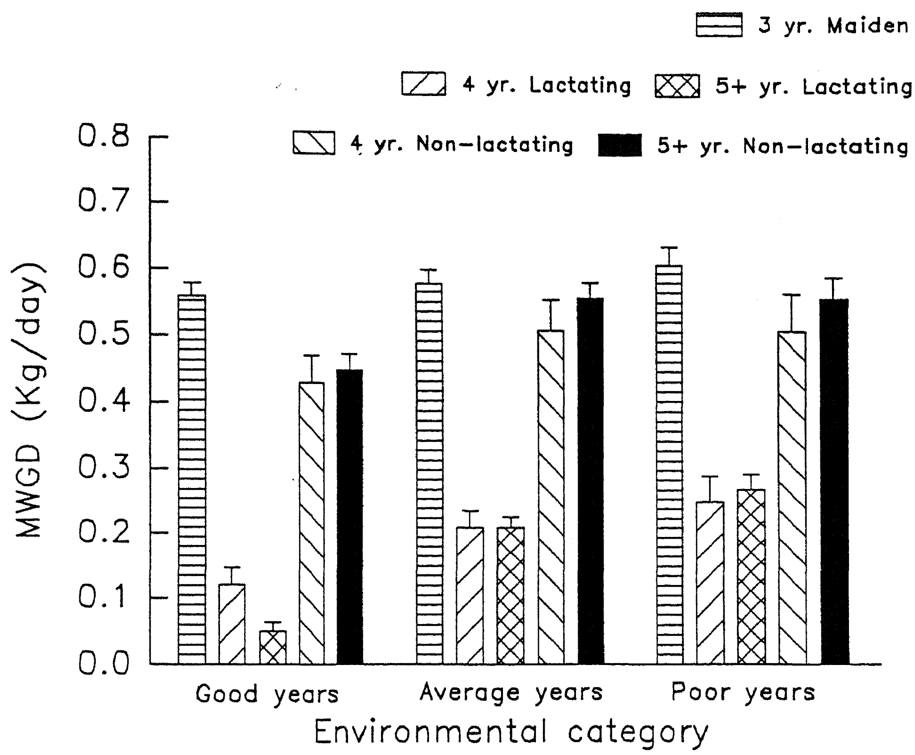

FIGURE 13

Interaction of AGEPLS by environmental category for MWGD of all genotypes from 1974 to 1990.

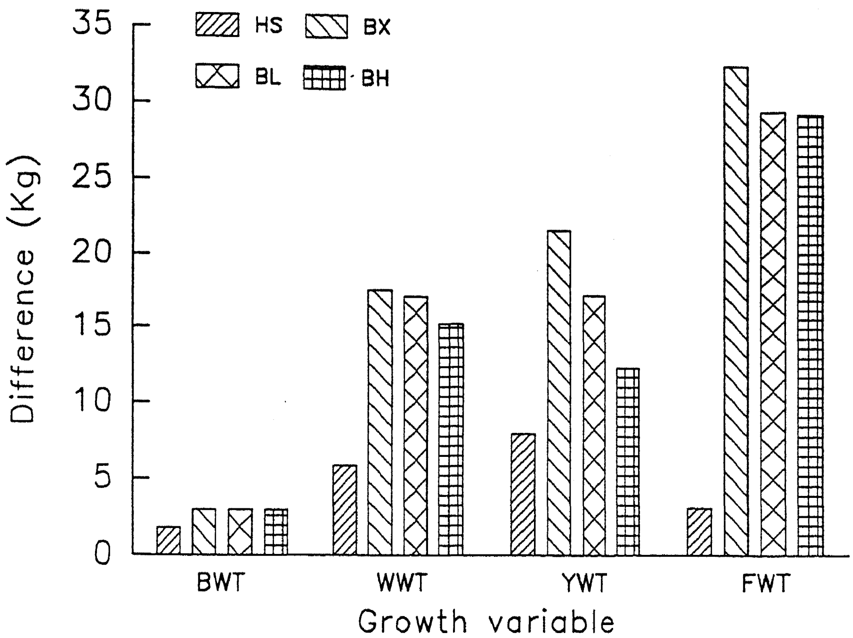

FIGURE 14
Difference in weight between male and female calves for BWT, WWT, YWT and FWT of all calf crops from 1974 to 1990.

BIBLIOGRAPHY

Aaron, D.K. and Thrift, F.A. (1990) Calving date verses calving interval as a measure of reproductive performance in Santa Gertrudis cows. *J.Anim.Sci.* **68**(1):20-21 (Abstr.).

Aaron, D.K., Thrift, F.A. and Nichols, C.G. (1990) Repeatability estimates for calving date and calving interval in Angus cattle. *J.Anim.Sci.* **68(1)**:226-227 (Abstr.).

Ahunu, B.K., Arthur, P.F., Danbaro, G. and Aboagye, G.S. (1993) Preweaning growth performance of West African Shorthorn cattle and their Jersey crossbreds in Ghana. *Trop.Anim.Hlth.Prod.* **25**:33-40.

Anderson, V.J., O'Rourke, P.K., Fordyce, G. and McCosker, T.H. (1988) Use of within herd information to improve conception rates in beef herds in northern Australia. *Proc.Aust.Soc.Anim.Prod.* **17**:138-141.

Andrews, L.G. (1976) Reproductive performance of beef cattle in the Northern Territory. MSc thesis, James Cook University of North Queensland.

Anonymous (1976) Notes on the research programmes. CSIRO Division of Animal Production, Rockhampton.

Anonymous (1983) Belmont technical committee report 1983. CSIRO Division of Tropical Animal Science, Rockhampton.

Anonymous (1993) The Brahman Sire Summary 1993. Compiled by ABRI for the Australian Brahman Breeders' Association Ltd.

Anonymous (1994) The Brahman Sire Summary 1994. Compiled by ABRI for the Australian Brahman Breeders' Association Ltd.

Arije, G.F. and Wiltbank, J.N. (1971) Age and weight at puberty in Hereford heifers. *J.Anim.Sci.* **33**:401-406.

Arthur, P.F., Hearnshaw, H., Kohun, P.J. and Barlow, R. (1994) Evaluation of *Bos indicus* and *Bos taurus* straightbreds and crosses. I. Post-weaning growth of steers in different environments. *Aust.J.Agric.Res.* **45**:783-794.

Azzam, S.M., Kinder, J.E., Nielsen, M.K., Werth, L.A., Gregory, K.E., Cundiff, L.V. and Koch, R.M. (1993) Environmental effects on neonatal mortality of beef calves. *J.Anim.Sci.* **71**:282-290.

B.I.F. (1981) Guidelines for uniform beef improvement programs. USDA, Extension Service, Program Aid, 1020. Revised.

Bailey, C.M. and Koh, Y.O. (1974) Maternal sib correlations for weaning weight in Hereford populations under diverse environments. *J.Anim.Sci.* **38**:923-927.

Bair, L.G., Wilson, L.L. and Ziegler, J.H. (1972) Effects of calf sex and age of dam on pre- and post-weaning performance of calves from an Angus-Holstein crossbred herd. *J.Anim.Sci.* **35**:1155-1159.

Baker, R.L. and Morris, C.A. (1984) A review of correlated responses to weight selection in beef cattle under different management and climatic conditions. In : *Proc.2nd World Congress on Sheep and Cattle Breeding*. Eds. J.H. Hofmeyr and E.H.H. Meyer, Pretoria, South Africa, p. 236-251.

Baker, R.L., Morris, C.A., Johnson, D.L., Hunter, J.C. and Hickey, S.M. (1991) Results of selection for yearling or 18-month weight in Angus and Hereford cattle. *Livest.Prod.Sci.* **29**:277-296.

Barlow, R. (1978) Biological ramifications of selection for pre-weaning growth in cattle. A review. *Anim.Breed.Abstr.* **46**:469-491.

Barlow, R. and O'Neill, G.H. (1978) Performance of Hereford and crossbred Hereford cattle in the subtropics of New South Wales : Growth of First-cross calves to weaning. *Aust.J.Agric.Res.* **29**:1313-1324.

Barlow, R. and O'Neill, G.H. (1980) Performance of Hereford and crossbred Hereford cattle in the subtropics of New South Wales : Genetic analysis of pre-weaning performance of first-cross calves. *Aust.J.Agric.Res.* **31**:417-427.

Barwick, S.A., Davis, G.P., Graser, H-U., Fuchs, W., Burrow, H.M. and Hammond, K. (1992) The value of reproduction and later weight criteria in selection in northern and southern Australian beef herds. *Proc.Aust.Assoc.Anim.Breed.Genet.* **10**:349-352.

Basarab, J.A., Rutter, L.M. and Day, P.A. (1993) The efficacy of predicting dystocia in yearling beef heifers: II. Using discriminant analysis. *J.Anim.Sci.* **71**:1372-1380.

Bean, K.G., Seifert, G.W., MacQueen, A. and Double, B.M. (1987) Effect of insecticide treatment for control of buffalo fly on weight gains of steers in coastal central Queensland. *Aust.J.Exp.Agric.* **27**:329-334.

Bellows, R.A. and Short, R.E. (1978) Effects of precalving feed level on birth weight, calving difficulty and subsequent fertility. *J.Anim.Sci.* **46**:1522-1528.

Berruecos, J.M. and Robinson, O.W. (1968) Preweaning growth in Brahmans. *J.Anim.Sci.* **27**:1124 (Abstr.)

Bichard, M. (1990) Changes in Quantitative Genetic Technology in Animal Breeding. *Proc.2nd Inter.Conf. on Quantitative Genetics*, 145-149.

Bluntzer, J.S., Forrest, D.W., Harms, P.G., Beverly, J.R. and Long, C.R. (1989) Effect of suckling manipulation on postpartum reproduction in primiparous Brahman-cross cows. *Theriogenology* **32**:893-899.

Bolton, R.C., Frahm, R.R., Castree, J.W. and Coleman, S.W. (1987a) Genotype x environment interactions involving proportion of Brahman breeding and season of birth I. Calf growth to weaning. *J.Anim.Sci.* **65**:42-47.

Bolton, R.C., Frahm, R.R., Castree, J.W. and Coleman, S.W. (1987b) Genotype x environment interactions involving proportion of Brahman breeding and season on birth II. Postweaning growth, sexual development and reproductive performance of heifers. *J.Anim.Sci.* **65**:48-55.

Boorman, A.J. and Hosegood, G.J. (1986) Turn off from cattle properties in Cape York Peninsula : improvement possibilities. *Proc.Aust.Soc.Anim.Prod.* **16**:155-158.

Bourdon, R.M. and Brinks, J.S. (1982) Genetic, environmental and phenotypic relationships among gestation length, birth weight, growth traits and age at first calving in beef cattle. *J.Anim.Sci.* **55**:543-553.

Bovard, K.P. and Weinland, B.T. (1973) Monthly weights of beef calves at weaning. *J.Anim.Sci.* **36**:198 (Abstr.)

BREEDPLAN Handbook (1991) Specialist School on Breedplan. University of New England, Armidale, unpublished manuscript.

Bronson, F.H. and Rissman, E.F. (1986) The biology of puberty. *Biol.Rev.* **61**:157-195.

Brown, C.J. (1960) Influence of year and season of birth, sex, sire and age of dam on weights of beef calves at 60, 120, 180 and 240 days of age. *J.Anim.Sci.* **19**:1062-1070.

Brown, M.A., Brown, A.H.Jr., Jackson, W.G. and Miesner, J.R. (1993a) Genotype x environment interactions in postweaning performance to yearling in Angus, Brahman and reciprocal cross calves. *J.Anim.Sci.* **71**:3273-3279.

Brown, M.A., Tharel, L.M., Brown, A.H.Jr., Jackson, W.G. and Miesner, J.R. (1993b) Genotype x environment interactions in preweaning traits of purebred and reciprocal cross Angus and Brahman calves on Common Bermudagrass and Endophyte-infected Tall Fescue Pastures. *J.Anim.Sci.* **71**:336-333.

Brown, M.A., Tharel, L.M., Brown, A.H.Jr., Jackson, W.G. and Miesner, J.R. (1993c) Milk production in Brahman and Angus cows on Endophyte-Infected Fescue and Common Bermudagrass. *J.Anim.Sci.* **71**:1117-1122.

Buck, N.G., Light, D., Rutherford, A., Miller, M., Rennie, T.W., Pratchett, D., Capper, B.S. and Trail, J.C.M. (1976) Environmental factors affecting beef cow reproductive performance in Botswana. *Anim.Prod.* **23**:357-363.

Buddenberg, B.J., Brown, C.J., Johnson, Z.B., Dunn, J.E. and Peterson, H.P. (1989) Heritability estimates of pregnancy rate in beef cows under natural mating. *J.Anim.Sci.* **67**:2589-2594.

Burris, M.J. and Priode, B.M. (1958) Effect of calving date on subsequent calving performance. *J.Anim.Sci.* **17**:527-533.

Burrow, H.M., Seifert, G.W. and Hetzel, D.J.S. (1991) Consequences of selection for weaning weight in Zebu, *Bos taurus* and Zebu x *Bos taurus* cattle in the Tropics. *Aust.J.Agric.Res.* **42**:295-307.

Butler, W.R. and Smith, R.D. (1989) Interrelationships between energy balance and postpartum reproductive function in dairy cattle. *J.Dairy Sci.* **72**:767-783.

Byerley, D.J., Staigmiller, R.B., Berardinelli, J.G. and Short, R.E. (1987) Pregnancy rates of beef heifers bred either on pubertal or third oestrus. *J.Anim.Sci.* **65**:645-650.

Cameron, N.D. (1993) Methodologies for estimation of genotype with environment interaction. *Livest.Prod.* **35**:237-249.

Cardellino, R. and Frahm, R.R. (1970) Age of dam adjustments for weaning weights of beef calves. *J.Anim.Sci.* **31**:161-162. (Abstr.)

Carroll, D.J., Jerred, M.J. and Grummer, R.R. (1990) Effects of fat supplementation and immature Alfalfa to concentrate ratio on plasma progesterone, energy balance and reproductive traits of dairy cattle. *J.Dairy Sci.* **73**:2855-2863.

Carruthers, T.D., Convey, E.M., Kesner, J.S., Hafs, H.D. and Cheng, K.W. (1980) The hypothalamo pituitary gonadotrophic axis of suckled and nonsuckled dairy cows postpartum. *J.Anim.Sci.* **51**:949-957.

Chenoweth, P.J. (1994) Aspects of reproduction in female *Bos indicus* cattle : a review. *Aust.Vet.J.* **71**:422-426.

Cobby, J.M. and Le Du, Y.L.P. (1978) On fitting curves to lactation data. *Anim.Prod.* **26**:127-133.

Couchman, R.C. (1983) Reproductive efficiency of heifers in the New Guinea highlands. *Trop.Anim.Hlth.Prod.* **15**:69-75.

Cravey, M.D. and Turner, J.W. (1990) Development of age of dam and sex adjustment factors for preweaning traits in Brangus cattle. In:*Beef Cattle Research in Texas*, 1989:p.13-18.

Creek, M.J. and Nestel, B.L. (1964) Animal production studies in Jamaica. III. The effect of dam age upon the 210-day weights of calves and the response of male and female calves to different environments. *J.Agric.Sci.* **62**:165-177.

Cubas, A.C., Berger, P.J. and Healey, M.H. (1991) Genetic parameters for calving ease and survival at birth in Angus field data. *J.Anim.Sci.* **69**:3952-3958.

Cundiff, L.V., Willham, R.L. and Pratt, C.A. (1966) Additive versus multiplicative correction factors for weaning weight in beef cattle. *J.Anim.Sci.* **25**:983-987.

D'Occhio, M.J., O'Neill, C.J. and Frisch, J.E. (1994) Improving the productivity of cattle in sub-tropical environments : Effects of crossbreeding on age and liveweight at puberty in Zebu, European and Zebu x European heifers. Strengthening research on animal reproduction and disease diagnosis in Asia through the application of immunoassay techniques. Bangkok, Thailand. IAEA-TECDOC-736:65-73.

Damon, R.A.Jr., Harvey, W.R., Singletary, C.B., McCraine, S.E. and Crown, R.M. (1961) Genetic anlaysis of crossbreeding beef cattle. *J.Anim.Sci.* **20**:849-857.

Davis, G.P. (1993) Genetic parameters for tropical beef cattle in northern Australia : a review. *Aust.J.Agric.Res.* **44**:179-198.

Davis, G.P., Corbet, N.J., Mackinnon, M.J., Hetzel, D.J.S., Entwistle, K.W. and Dixon, R. (1993) Response in female fertility and calf growth to selection for pregnancy rate in tropical beef cattle. *Aust.J.Agric.Res.* **44**:1509-1521.

De Nise, R.S.K., Torabi, M., Ray, D.E. and Rice, R. (1988) Genetic parameter estimates for preweaning traits of beef cattle in a stressful environment. *J.Anim.Sci.* **66**:1899-1906.

De Nise, R.S.K. and Torabi, M. (1989) Genetic parameter estimates for postweaning traits of beef cattle in a stressful environment. *J.Anim.Sci.* **67**:2619-2626.

De Rouen, S.M., Franke, D.E., Morrison, D.G., Yatt, W.E., Coombs, D.F., White, T.W., Humes, P.E. and Green, B.B. (1994) Prepartum body condition and weight influences on reproductive performance of first-calf beef cows. *J.Anim.Sci.* **72**:1119-1125.

Dearborn, D.D., Kock, R.M., Cundiff, L.V., Gregory, K.E. and Dickerson, G.E. (1973) An analysis of reproductive traits in beef cattle. *J.Anim.Sci.* **36**:1032-1040.

Deese, R.E. and Koger, M. (1965) Maternal effects on preweaning growth rate in cattle. *J.Anim.Sci.* **26**:250-253.

Deese, R.E. and Koger, M. (1967) Heritability of fertility in Brahman crossbred cattle. *J.Anim.Sci.* **26**:984-987.

Deutscher, G.H., Stotts, J.A. and Nielsen, M.K. (1991) Effects of breeding season length and calving season on range beef cow productivity. *J.Anim.Sci.* **69**:3453-3460.

Dinkel, C.A., Tucker, W.L. and Marshall, D.M. (1990) Sources of variation in beef cattle weaning weight. *Can.J.Anim.Sci.* **70**:761-769.

Domínguez, L.R.R., Ríos, L.G. and Flores, M.L.A. (1993) Environmental effects on the reproductive performance and fertility of American Brown Swiss cows in the subhumid tropics. *Anim.Breed Abstr.* **61**:541.

Doogan, V.J., Fordyce, G., Shepherd, R.K., James, T.A. and Holroyd, R.G. (1991) The relationship between liveweight, growth from weaning to mating and conception rate of *Bos indicus* cross heifers in the dry tropics of North Queensland. *Aust.J.Exp.Agric.* **31**:139-144.

Dzuik, P.J. and Bellows, R.A. (1983) Management of reproduction of beef cattle, sheep and pigs. *J.Anim.Sci.* **57**(Suppl. 2):355-379.

Eduvie, L.O. and Dawuda, P.M. (1986) Effect of suckling on reproductive activities on Bunagi cows during the postpartum period. *J.Agric.Sci.Camb.* **107**:235-238.

Elings, J.T., Johnson, W.H. and Bennett, L.F. (1971) Effect of age on ADG to weaning in beef cattle. *J.Anim.Sci.* **33**:198 (Abstr.)

Entwistle, K.W. (1983) Factors influencing reproduction in beef cattle in Australia. *Aust.Meat Res.Comm.Rev.* No.43.

Entwistle, K.W. (1984) Practical considerations in beef cattle reproductive programs. In: *Proc.Refresher Course for Veterinarians*, **No. 86**. University of Sydney, Post Graduate Committee in Veterinary Science:p.311-330.

Entwistle, K.W. (1989) Advances in animal productive in the tropics. In: *Proc.Refresher Course for Veterinarians*, **No. 121**. University of Sydney, Post Graduate Committee in Veterinary Science:p.141-158.

Falconer, D.S. (1989) Introduction to Quantitative Genetics (3rd Ed.) New York:Longman Scientific and Technical, John Wiley and Sons.

Fordyce, G., James, T.H., Holroyd, R.G., Beaman, N.J., Mayer, R.J. and O'Rourke, P.K. (1993a) The performance of Brahman-Shorthorn and Sahiwal-Shorthorn cattle in the dry tropics of northern Queensland. 3. Birth weights and growth to weaning. *Aust.J.Exp.Agric.* **33**:119-127.

Fordyce, G., Loxton, I.D., Holroyd, R.G. and Mayer, R.J. (1993b) The performance of Brahman-Shorthorn and Sahiwal-Shorthorn cattle in the dry tropics of northern Queensland. 4. Postweaning growth and carcass traits. *Aust.J.Exp.Agric.* **33**:531-539.

Fordyce, G., Saithanoo, S. and Goddard, M.E. (1989) Factors affecting mature size and dry-season weight loss in *Bos indicus* cross cows in northern Queensland. *Aust.J.Agric.Res.* **36**:1169-1180.

Fordyce, G., Tyler, R. and Anderson, V.J. (1990) Effect of reproductive status, body condition and age of *Bos indicus* cross cows early in a drought on survival and subsequent reproductive performance. *Aust.J.Exp.Agric.* **25**:315-322.

Foster, A.H. and Blight, G.W. (1984) Liveweight response of cattle grazing native pasture in south-east Queensland when supplemented with urea molasses in winter and spring. *Tropical Grasslands* **18**:131-137.

Francoise, J.J., Vogt, D.W. and Nolan, J.C.Jr. (1973) Hertiability of genetic and phenotypic correlations among some economically important traits in beef cattle. *J.Anim.Sci.* **36**:635-639.

Franke, D.E. (1980) Breed and heterosis effect of American zebu cattle. *J.Anim.Sci.* **50**:1206-1214.

Franke, D.E., Koger, M. and Cruz, V. (1973) Reproduction in Brahman cattle. *J.Anim.Sci.* **36**:198 (Abstr.).

Franke, D.E. and Oviedo (1992) Breed type, age of cow and sex of calf interaction in preweaning data. *J.Anim.Sci.* **70**(Suppl. 1):4 (Abstr.)

Freund, J.E. and Walpole, R.E. (1987) Mathematical statistics (4th Ed.) New Jersey:Prentice/Hall International, Inc.

Frisch, J.E. (1972) Comparative drought resistance of *Bos indicus* and *Bos taurus* crossbred herds in central Queensland. 1. Relative weight and weight changes of maiden heifers. *Aust.J.Exp.Agric.Anim.Husb.* **12**:231-233.

Frisch, J.E. (1973) Comparative drought resistance of *Bos indicus* and *Bos taurus* crossbred herds in central Queensland. 2. Relative mortality rate, calf birth weights and weight changes of breeding cows. *Aust.J.Exp.Agric.Anim.Husb.* **13**:117-126.

Frisch, J.E. (1975) The relative incidence and effect of Bovine Infectious Keratoconjunctivitis in *Bos indicus* and *Bos taurus* cattle. *Anim.Prod.* **21**:265-274.

Frisch, J.E. (1981) Correlated responses in cattle selected in a stressful environment. PhD thesis, University of Queensland.

Frisch, J.E. (1987) Physiological reasons for heterosis in growth of *Bos indicus* x *Bos taurus*. *J.Agric.Sci.Camb.* **109**:213-230.

Frisch, J.E. (1993) What is the most practical and effective method for genetic evaluation of reproductive performance in a beef cattle breeding program? (Paper read at the Australian Beef Improvement Association Meeting, Armidale, July 1993).

Frisch, J.E. and Hunter, R.A. (1990a) Influence of the growth promotant Synovex H® on growth, resistance to parasites and reproduction of cattle heifers of three breeds. *J.Agric.Sci.Camb.* **114**:107-113.

Frisch, J.E. and Hunter, R.A. (1990b) Interaction of Compudose 200® and resistance to parasites on growth of steers of two cattle breeds. *J.Agric.Sci.Camb.* **115**:259-264.

Frisch, J.E., Munro, R.K. and O'Neill, C.J. (1987) Some factors related to calf crops of Brahman, Brahman crossbred and Hereford x Shorthorn cows in a stressful tropical environment. *Anim.Reprod.Sci.* **15**:1-26.

Frisch, J.E., O'Neill, C.J. and Burrow, H.M. (1984) The incidence and effect of poisoning with *Lantana camara* in different cattle breeds. *J.Agric.Sci.Camb.* **102**:191-195.

Frisch, J.E. and Vercoe, J.E. (1977) Food intake, eating rate, weight gains, metabolic rate and efficienty of feed utilisation in *Bos taurus* and *Bos indicus* crossbred cattle. *Anim.Prod.* **25**:343-358.

Frisch, J.E. and Vercoe, J.E. (1981) Changes in fasting metabolism of cattle as a consequence of selection for growth rate. In: *Energy Metabolism.* Ed. L.E. Mount (London:Butterworths) EAAP Publication **26**:431-434.

Frisch, J.E. and Vercoe, J.E. (1982) Consideration of adaptive and productive components of productivity in breeding beef cattle for tropical Australia. *Proc.2nd World Cong. on Genet.App. in Livest.Prod.* Section RT-E:307-321.

Frisch, J.E. and Vercoe, J.E. (1984) An analysis of growth of different cattle genotypes reared in different environments. *J.Agric.Sci.Camb.* **103**:137-153.

Galina, C.S. and Arthur, G.H. (1989a) Review of cattle reproduction in the tropics. Part 1. Puberty and age at first calving. *Anim.Breed Abstr.* **57**:584-590.

Galina, C.S. and Arthur, G.H. (1989b) Review of cattle reproduction in the tropics. Part 2. Parturition and calving intervals. *Anim.Breed Abstr.* **57**:679-686.

Galina, C.S. and Arthur, G.H. (1989c) Review of cattle reproduction in the tropics. Part 3. Puerperum. *Anim.Breed Abstr.* **57**:899-910.

Ghosh, A., Alan, M.G.S. and Akbar, M.A. (1993) Effect of urea-molasses-mineral block supplementation on postpartum ovarian activity in zebu cows. *Anim.Prod.Sci.* **31**:61-67.

Goddard, M.E., Entwistle, K.W. and Dixon, R. (1980) Variables affecting pregnancy rate in *Bos indicus* cross cows. *Proc.Aust.Soc.Anim.Prod.* **13**:65-67.

Gómez, I.A., Barrenche, R.G., Conley, G. and Posada, S. (1974) Environmental effects on weaning weight of Brahman cattle in Colombia. *Anim.Breed Abstr.* **42**:5.

Graham, T.W.G., Wood, S.J., Knight, J.L. and Blight, G.W. (1983) Urea and molasses as a winter supplement for weaner steers grazing improved pastures in central Queensland. *Tropical Grasslands* **17**:11-20.

Graser, H-U. and Hammond, K. (1985) Mixed model procedures for the Australian Beef Industry. I. Multiple trait model for estimation of breeding values for 200-day and final weights of cattle. *Aust.J.Agric.Res.* **35**:527-555.

Greer, R.C., Whitman, R.W., Staigmiller, R.B. and Anderson, D.C. (1983) Estimating the impact of management decisions on the occurrence of puberty in beef heifers. *J.Anim.Sci.* **56**:30-39.

Haile-Marian, M. and Kassa-Mersha, H. (1994) Genetic and environmental effects on age at first calving and calving interval of naturally bred Boran (zebu) cows in Ethiopia. *Anim.Prod.* **58**:329-334.

Hall, H.T.B. (1985) Disease and Parasites of Livestock in the Tropics, (2nd) Intermediate Tropical Agriculture Series, Ed. W.J.A. Payne:London,Longman.

Hammond, K. (1989) Genetic evaluation. In: *Proc.Refresher Course for Veteriarians*, **No. 121**. University of Sydney, Post Graduate Committee in Veterinary Science:p.365-383.

Hansen, L.B., Freeman, A.E. and Berger, P.J. (1983) Association of heifer fertility with cow fertility and yield in dairy cattle. *J.Dairy Sci.* **66**:306-314.

Hansen, P.J. (1991) The relationship between energy status and the resumption of estrus cycles in cattle. *Revista Brasileira de Reproducao Animal* (No. 3 Supp.) : 200-209.

Hanzen, Ch. (1986) Endocrine regulation of postpartum ovarian activity in cattle : a review. *Reprod.Nutr.Develop.* **26**:1219-1239.

Harrison, R.O., Ford, S.P., Young, J.W., Conley, A.J. and Freeman, A.E. (1990) Increased milk production verses reproductive and energy status of high producing dairy cows. *J.Dairy Sci.* **73**:2749-2758.

Harvey, W.R. (1987) Users Guide for LSMLMW PC-1 Version. Mixed Model Least-Squares and Maximum Likelihood Computer Program. Unpublished manuscript.

Harwin, G.O., Brinks, J.S. and Stonaker, H.H. (1966) Genetic and environmental interactions affecting weaning weights of Hereford calves. *J.Anim.Sci.* **25**:779-782.

Harwin, G.O. and Lombard, J.H. (1974) Intensification of the beef-cow herd. *S.Afr.J.Anim.Sci.* **4**:247-258.

Henderson, C.R. (1973) Sire evaluation and genetic trends. In: *Anim.Breed.Genet.Symp.* in honour of Dr. J.L. Lush, Illinois : American Society of Animal Science,p.10-28.

Hentges, J.F. and Howes, J.R. (1963) Milk production. In: *Crossbreeding Beef Cattle.* Ed. T.J. Cunha, M. Koger and A.C. Warwick. Gainesville, University of Florida Press:p.93-97.

Hetzel, D.J.S., Mackinnon, M.J., Dixon, R. and Entwistle, K.W. (1989) Fertility in a tropical beef herd divergently selected for pregnancy rate. *Anim.Prod.* **49**:73-81.

Hetzel, D.J.S., Quaas, R.L., Seifert, G.W. Bean, K.G., Burrow, H.M. and Aspden, W.J. (1990) Genetic parameters for growth of tropical beef cattle. *Proc.8th Aust.Assoc.Anim.Breed.Genet.* **8**:517-520.

Hohenboken, W.D., Hauser, E.R., Chapman, A.B. and Cundiff, L.V. (1971) Relationships among lactation and progeny traits. *J.Anim.Sci.* **33**:202 (Abstr.).

Holmes, J.H.G., Takken, A. and Seifert, G.W. (1968) Milk production and calf growth rate in Hereford, Africander-Shorthorn and Brahman-Shorthorn cattle in Queensland. *Proc.Aust.Soc.Anim.Prod.* **7**:163-171.

Holroyd, R.G. (1977) Reproductive performance of beef cattle in northern Queensland. MSc thesis, James Cook University of North Queensland.

Holroyd, R.G. (1985) Aspects of reproduction in *Bos indicus* genotypes. PhD thesis, James Cook University of North Queensland.

Holroyd, R.G., James, T.A., Doogan, V.J., Fordyce, G. and O'Rourke, P.K. (1990a) The performance of Brahman-Shorthorn and Sahiwal-Shorthorn beef cattle in the dry tropics of northern Queensland. 1. Reproductive rates and liveweights of F_1 and backcross females. *Aust.J.Exp.Agric.* **30**:717-725.

Holroyd, R.G., James, T.A., Doogan, V.J., Fordyce, G., Tyler, R. and O'Rourke, P.K. (1990b) The performance of Brahman-Shorthorn and Sahiwal-Shorthorn beef cattle in the dry tropics of northern Queensland. 2. Reproductive rates and liveweights of F_2 *et seq* females. *Aust.J.Exp.Agric.* **30**:727-733.

Holroyd, R.G., Mason, G.W.J., Loxton, I.D., Knights, P.T. and O'Rourke, P.K. (1988) Effects of weaning and supplementation on performance of Brahman cross cows and their progeny. *Aust.J.Exp.Agric.* **28**:11-20.

Holroyd, R.G., O'Rourke, P.K., Clark, M.R. and Loxton, I.D. (1983) Influence of pasture type and supplement on fertility and liveweight of cows, and progeny growth rate in the dry tropics of northern Queensland. *Aust.J.Exp.Agric.Anim.Husb.* **23**:4-13.

Holroyd, R.G., O'Rourke, P.K., Tyler, R., Stephenson, H.P., Mason, G.W.J. and Schroter, K.L. (1990c) Effects of different weaning strategies on postweaning growth rate, mortality and fertility of *Bos indicus* cross cattle. *Aust.J.Exp.Agric.* **30**:1-6.

Hungerford, T.G. (1990) Diseases of Livestock (9th Ed.) Sydney:McGraw-Hill Book Company.

Hunter, R.A. (1991) Strategic supplementation for survival, reproduction and growth of cattle. In: *Proc.2nd Graz.Livest.Nutr.Conf.*, Colorado : 32-47.

Hunter, R.A. and Buck, N. (1992) Nutritional and climatic limits to beef production in the tropics. *World Anim.Sci. : Beef Cattle Production* Chap. 20:379-394.

Hurley, W.L. and Doane, R.M. (1989) Recent developments in the roles of vitamins and minerals in reproduction. *J.Dairy Sci.* **72**:784-804.

Iloeje, M.U. (1986) Components of variance for growth traits among zebu and South Devon beef cattle in southwestern Nigeria. *Livest.Prod.Sci.* **14**:231-238.

Itulya, S.B., Ray, D.E., Roubicek, C.B. and Benson, C.R. (1987) Genetic parameters, maternal ability and related selection criteria for unsupplemented Hereford range cows. *J.Anim.Sci.* **64**:1630-1637.

Jasiorowski, H.A. (1983) Cattle Production System of the World. In: *Beef Cattle Science Handbook*. Ed. F.H. Baker:p.16-23.

Jeffery, H.B., Berg, R.T. and Harwin, R.T. (1971) Factors affecting preweaning performance in beef cattle. *Can.J.Anim.Sci.* **51**:561-577.

Johnson, D.L. and Garrick, D.J. (1990) Data collection, processing and predicition of breeding values. *Proc.4th World Cong.Genet.App. to Livest.Prod.* **XV**:337-346.

Joubert, D.M. (1963) Puberty in female farm animals. *Anim.Breed Abstr.* **31**:295-306.

Keller, D.G. and Brinks, J.S. (1978) Mating system by environment interaction for weaning weight in Hereford cattle. *J.Anim.Sci.* **46**:54-59.

Kennedy, J.F. and Chirchir, G.I.K. (1971) A study of the growth rate of F_2 and F_3 Africander cross, Brahman cross and British cross cattle from birth to 18 months in a tropical environment. *Aust.J.Exp.Agric.Anim.Husb.* **11**:593-598.

King, J.W.B. and Smith, C. (1984) Strategies for estimating genetic change. In : *Proc.World Cong. on Sheep and Beef Cattle Breeding*. Eds. R.A. Barton and W.C. Smith. Vol I:231-238.

Kinghorn, B. (1992) Principles of Estimated Breeding Values. In : *Animal Breeding:The Modern Approach*. Eds. K. Hammond, H-U. Graser and C.A. McDonald. Post-Grad. Foundation in Vet.Sci., University of Sydney, p. 47-55.

Koch, R.M. (1972) The role of maternal effects in animal breeding : VI. Maternal effects in beef cattle. *J.Anim.Sci.* **35**:1316-1323.

Koch, R.M., Gregory, K.E. and Cundiff, L.V. (1982) Critical analysis of selection methods and experiments in beef cattle and consequences upon selection programs applied. *Proc.2nd World Cong. on Genet.App.Livest.Prod.* Section PS-VIb-4:514-526.

Koger, M., Reynolds, W.L., Kirk, W.G., Peacock, F.M. and Warnick, A.C. (1962) Reproductive performance of crossbred and straightbred cattle on different pasture programs in Florida. *J.Anim.Sci.* **21**:14-19.

Lammond, D.R. (1970) The influence of undernutrition on reproduction in the cow. *Anim.Breed Abstr.* **38**:359-372.

Lapworth, J.W., Bean, K.G., Seifert, G.W. and Rudder, T.H. (1976) Factors affecting the performance of steers grown under commercial conditions in a sub-tropical environment. *Aust.J.Exp.Agric.Anim.Husb.* **16**:636-639.

Laster, D.B., Glimp, H.A. and Gregory, K.E. (1972) Age and weight at puberty and conception in different breeds and breed-crosses of beef heifers. *J.Anim.Sci.* **34**:1031-1036.

Laster, D.B., Glimp, H.A. and Gregory, K.E. (1973a) Effects of early weaning on postpartum reproduction of cows. *J.Anim.Sci.* **36**:734-740.

Laster, D.B., Glimp, H.A., Cundiff, L.V. and Gregory, K.E. (1973b) Factors affecting dystocia and the effect of dystocia on subsequent reproduction in beef cattle. *J.Anim.Sci.* **36**:695-705.

Lesmeister, J.L., Burfening, P.J. and Blackwell, R.L. (1973) Date of first calving in beef cows and subsequent calf production. *J.Anim.Sci.* **36**:1-6.

Loxton, I.D., Murphy, G.M. and Toleman, M.A. (1983) Effect of superphosphate application on the phosphorus status of breeding cattle grazing Townsville stylo based pastures in northern Queensland. *Aust.J.Exp.Agric.Anim.Husb.* **23**:340-347.

Lubritz, D.L., Forrest, K. and Robinson, O.W. (1989) Age of cow and age of dam effects on milk production of Hereford cows. *J.Anim.Sci.* **67**:2544-2549.

Lubritz, D.L., Humes, P.E., Aguel, C.F. and Morrison, D.G. (1987) Genetic and environmental factors influencing the growth patterns of upgraded Chianina cows. *J.Anim.Sci.* **65**(1):9 (Abstr.)

Lusby, K.S., Wettemann, R.P. and Turman, E.J. (1981) Effects of early weaning calves from first-calf heifers on calf and heifer performance. *J.Anim.Sci.* **53**:1193-1197.

MacGregor, R.G. and Swanepoel, F.J.C. (1992) The relationship between body mass and fertility in Bonsmara breeding females. *S.Afr.J.Anim.Sci.* **22**:64-69.

Mackinnon, M.J. (1988) Genetic and environmental effects on fertility of cattle in a sub-tropical environment. MSc. thesis, James Cook University of North Queensland.

Mackinnon, M.J., Hetzel, D.J.S. and Taylor, J.F. (1989) Genetic and environmental effects on the fertility of beef cattle in a tropical environment. *Aust.J.Agric.Res.* **40**:1085-1097.

Mackinnon, M.J., Meyer, K. and Hetzel, D.J.S. (1991) Genetic variation and covariation for growth, parasite resistance and heat tolerance in tropical cattle. *Livest.Prod.Sci.* **27**:105-122.

MacMillan, K.L. (1983) Post-partum interval to oestrus in monozygous twin cows and possible effects of maternal bonding. *N.Z.J.Anim.Res.* **26**:451-454.

Madalena, F.E. and Hinojosa, C. (1976) Reproductive performance of zebu compared with Charolais x zebu females in a humid tropical environment. *Anim.Prod.* 23:55-62.

Manfredi, E.J., San Cristobal, M. and Foulley, J.L. (1991) Some factors affecting the estimation of genetic parameters for cattle dystocia under a threshold model. *Anim.Prod.* 53:151-156.

Martin, L.C., Brinks, J.S., Bourdon, R.M. and Cundiff, L.V. (1992) Genetic effects on beef heifer puberty and subsequent reproduction. *J.Anim.Sci.* **70**:4006-4017.

Martojo, H., Pace, J.E. and Franke, D.E. (1972) Factors influencing weaning weight in BCIA herds. *J.Anim.Sci.* **35**:179 (Abstr.)

Maurer, R.R. and Echternkamp, S.E. (1985) Repeat-breeder females in beef cattle : influences and causes. *J.Anim.Sci.* **61**:624-636.

McCarter, M.N., Buchanan, D.S. and Frahm, R.R. (1990) Comparison of crossbred cows containing various proportions of Brahman in spring or fall calving systems. 1. Productivity as two-year-olds. *J.Anim.Sci.* **68**:1547-1552.

McCarter, M.N., Buchanan, D.S. and Frahm, R.R. (1991a) Comparison of crossbred cows containing various proportions of Brahman in spring or fall calving systems. 2. Milk production. *J.Anim.Sci.* **69**:77-84.

McCarter, M.N., Buchanan, D.S. and Frahm, R.R. (1991b) Comparison of crossbred cows containing various proportions of Brahman in spring or fall calving systems. 3. Productivity as three, four and five year olds. *J.Anim.Sci.* **69**:2754-2761.

McCarter, M.N., Buchanan, D.S. and Frahm, R.R. (1991c) Comparison of crossbred cows containing various proportions of Brahman in spring or fall calving systems. 4. Effects of gentoype x environment interaction on lifetime productivity of young cows. *J.Anim.Sci.* **69**:3977-3982.

McCosker, T.H., Eggington, A.R. and Doyle, F.W. (1984) Observations on-post-weaning performance of Brahman cross animals in the Darwin district of the Northern Territory. *Proc.Aust.Soc.Anim.Prod.* **15**:452-455.

McSweeney, C.S., Kennedy, P.M., D'Occhio, M.J., Fitzpatrick, L.A., Reid, D. and Entwistle, K.W. (1993) Reducing post-partum anoestrous interval in first-calf *Bos indicus* crossbred beef heifers. II. Responses to weaning and supplementation. *Aust.J.Agric.Res.* **44**:1063-1077.

Meijering, A. (1984) Dystocia and stillbirths in cattle - A review of causes, relations and implications. *Livest.Prod.Sci.* **11**:143-177.

Meyer, K. (1990) Present status of knowledge about statistical procedurres and algorithms to estimate variance and covariance components. *Proc.4th World Cong.Genet.App.Livest.Prod.* XII: 407-418.

Meyer, K. (1992) Variance components due to direct and maternal effects for growth traits of Australian beef cattle. *Livest.Prod.Sci.* **31**:179-204.

Meyer, K., Hammond, K., Parnell, P.F., Mackinnon, M.J. and Sivarajasigam (1990) Estimates of heriability and repeatability for reproductive traits in Australia beef cattle. *Livest.Prod.Sci.* **25**:15-30.

Molina, S.R., Deaton, O. and Munoz, H. (1982) Production potential of the Romosinuano and its use in crossbreeding for beef. *Trop.Anim.Prod.* **7**:257-261.

Montgomery, G.W., Davis, G.H. and Hurrell, G.A. (1980) Interval from calving to first oestrus in autumn- and spring-calving herds in the same locality. *Proc.N.Z.Soc.Anim.Prod.* **40**:280-284.

Montgomery, G.W., Scott, I.C. and Hudson, N. (1985) An interaction between season of calving and nutrition on the resumption of ovarian cycles in post-partum beef cattle. *J.Reprod.Fert.* **73**:45-50.

Moore, C.P. and da Rocha, C.M.C. (1983) Reproductive performance of Gyr cows : The effect of weaning age of calve and postpartum energy intake. *J.Anim.Sci.* **57**:807-814.

Morris, C.A. (1980) A review of relationships between aspects of reproduction in beef heifers and their lifetime production. 2. Assocations with relative calving date and with dystocia. *Anim.Breed.Abstr.* **48**:753-767.

Morris, C.A., Bennett, G.L., Baker, R.L. and Carter, A.H. (1986) Birth weight, dystocia and calf mortality in some New Zealand beef breeding herds. *J.Anim.Sci.* **62**:327-343.

Morris, C.A., Baker, R.L., Hickey, S.M., Johnson, D.L., Cullen, N.J. and Wilson, J.A. (1993) Evidence of genotype by environment interaction for reproductive and maternal traits in beef cattle. *Anim.Prod.* **56**:69-83.

Mrode, R.A. (1988) Selection experiment in beef cattle. Part 2. A review of responses and correlated responses. *Anim.Breed.Abstr.* **56**:155-167.

Mwandotto, B.A.J., Carles, A.B. and Cartwright, T.C. (1988) Weaning and 18-month weights of Boran, East African Shorthorn Zebu and Sahiwal breeds or crosses in Kenya. *Trop.Agric.(Trinidad)* **65**:257-264.

Naazie, A., Makarechian, M.M. and Berg, R.T. (1989) Factors influencing calving difficulty in beef heifers. *J.Anim.Sci.* **67**:3243-3249.

NBRS Recording Manual (1982) The National Beef Recording Scheme, University of New England. Unpublished manuscript.

Nelms, G.E. and Bogart, R. (1956) The effect of birthweight, age of dam and time of birth on suckling gains of beef calves. *J.Anim.Sci.* **15**:662-666.

Neville, W.E.Jr. (1962) Influence of dams milk production and other factors on 120 and 240-day weight of Hereford calves. *J.Anim.Sci.* **21**:315-320.

Neville, W.E.Jr., Richardson, K.L., Williams, D.J.III. and Utley, P.R. (1987) Cow breeding and calf growth performances as affected by pregnancy status the previous year. *J.Anim.Sci.* **65**:345-350.

Neville, W.E.Jr., Warren, E.P. and Griffey, W.A. (1974) Estimates of age effects on milk production in Hereford cows. *J.Anim.Sci.* **38**:1-5.

Newman, S. and Deland, M.P. (1991) Lifetime productivity of crossbred cows. 2. Age and weight at first oestrus, calf birth weight, assisted calvings, calving interval and reproduction rate. *Aust.J.Exp.Agric.* **31**:293-300.

Nicholls, P.J. and Tyrrell, R.N. (1980) Analysis of binary response data by generalised linear models. *Proc.Aust.Soc.Anim.Prod.* **13**:337-340.

Nicol, D.C., Graser, H-U., Tier, B. and Hammond, K. (1985) Breedplan - a new within-herd evaluation system for the National Beef Recording Scheme. *Proc.Aust.Assoc.Anim.Breed.Genet.* **5**:151-153.

Notter, D.R. (1988) Evaluating and reporting reproductive traits. *Proc.Beef Improv.Fed.Res.Symp. and Anim.Mtg.*, Albuquerque : p.21-42.

Notter, D.R. (1991) Accommodation of genotype x environment interactions in national genetic evaluation programs. *Proc.Aust.Assoc.Anim.Breed.Genet.* **9**:255-260.

Notter, D.R., Cundiff, L.V., Smith, G.M., Laster, D.B. and Gregory, K.E. (1978) Characterisation of biological types of cattle. VII. Milk production in young cows and transmitted and maternal effects on preweaning growth of progeny. *J.Anim.Sci.* **46**:908-921.

Notter, D.R. and Hohenboken, W.D. (1990) Industry breeding structures for effecting and evaluating genetic improvement. *Proc. 4th World Cong.Genet.App.Livest.Prod.* XV:347-356.

Oikawa, T., Schneeberger, M., Tier, B., Hammond, K. and Notter, D.R. (1991) The impact on EBV's of sex differences in variation in post-weaning growth of beef cattle. *Proc.Aust.Assoc.Anim.Breed.Genet.* **9**:247-250.

Oltenacu, P.A., Frick, A. and Lindhé, B. (1991) Relationship of fertility to milk yield in Swedish cattle. *J.Dairy Sci.* **74**:264-268.

Olsen, J.D., Gideon, J., Hopkin, W. and Wiltbank, J.N. (1993) Factors affecting pregnancy rate in 2 year old heifers for their second calf. *Proc.West Sect., Amer.Soc.Anim.Sci.* **44**:352-355.

O'Rourke, P.K. (1986) The statistical analysis of reproductive data from grazing experiments. *Proc.Aust.Soc.Anim.Prod.* **16**:65-77.

O'Rourke, P.K., Doogan, V.J., McCosker, T.H. and Eggington, A.R. (1991a) Prediction of conception rate in extensive beef herds in north-western Australia. I. Seasonal mating and efficient management. *Aust.J.Exp.Agric.* **31**:1-7.

O'Rourke, P.K., Doogan, V.J., Robertson, D.J. and Cooke, D. (1991b) Prediction of conception rate in extensive beef herds in north-western Australia. II. Continuous mating and minimal management. *Aust.J.Exp.Agric.* **31**:9-14.

O'Rourke, P.K., Esdale, C.R., Howitt, C.J. and Rudder, T.H. (1992) Productivity of Hereford, highgrade Simmental and Belmont Red beef herds in central Queensland. 3. Explanatory models for pregnancy rate. *Aust.J.Exp.Agric.* **32**:563-568.

O'Rourke, P.K., Winks, L. and Kelly, A.M. (1992) North Australia beef producer survey 1990. QDPI, Brisbane, Australia.

Osoro, K. and Wright, I.A. (1992) The effect of body condition, liveweight, breed, age, calf performance, and calving date on reproductive performance of spring-calved beef cows. *J.Anim.Sci.* **70**:1661-1666.

Pahnish, D.F., Roberson, R.L., Taylor, R.L., Brinks, J.S., Clark, R.T. and Roubicek, C.B. (1964) Genetic analysis of economic traits measured in range-raised Herefords at preweaning and weaning ages. *J.Anim.Sci.* **23**:562-568.

Patterson, D.J., Perry, R.C., Kiracofe, G.H., Bellows, R.A., Staigmiller, R.B. and Corah, L.R. (1992) Management considerations in heifer development and puberty. *J.Anim.Sci.* **70**:4018-4035.

Peacock, F.M., Kirk, W.G. and Koger, M. (1969) Reproduction and growth in Brahman, Shorthorn and crossbred cattle. *J.Anim.Sci.* **29**:11 (Abstr.)

Pell, E.W. and Thayne, W.V. (1978) Factors influencing weaning weight and grade of West Virginia beef calves. *J.Anim.Sci.* **46**:596-603.

Pinney, D.O., Stephens, D.F. and Pope, L.S. (1972) Lifetime effects of winter supplemental feed level and age at first parturition on range beef cows. *J.Anim.Sci.* **34**:1067-1074.

Plasse, D., Warnick, A.C. and Koger, M. (1968) Reproductive behaviou of *Bos indicus* females in a subtropical environment. I. Puberty and ovulation frequency in Brahman x British heifers. *J.Anim.Sci.* **27**:94-100.

Ponzoni, R.W. (1992) Which trait for genetic improvement of beef cattle reproduction:calving rate or calving day. *J.Anim.Breed.Genet.* **109**:119-128.

Ponzoni, R.W. and Gifford, D.R. (1994) Reproductive and some peri-natal variablies in a mixed breed beef cattle herd. *J.Anim.Breed.Genet.* **111**:52-64.

Preston, T.R. and Willis, M.R. (1974) Intensive Beef Production, Oxford : Pergamon Press.

Rahnefeld, G.W., Weiss, G.M., Fredeen, H.T., McKay, R.M., Lawson, J.E., Newman, J.A. and Bailey, D.R.C. (1991) Reproductive efficiency of F_1 and reciprocal backcross beef cows under contrasting environments. *Can.J.Anim.Sci.* **71**:969-985.

Randel, R.D. (1990) Nutrition and postpartum rebreeding in cattle. *J.Anim.Sci.* **68**:853-862.

Ray, D.E., Itulya, S.B., Roubicek, C.B. and Benson, C.R. (1989) Pregnancy rate, calf mortality and calving date in unsupplemented Hereford range cows. *Livest.Prod.Sci.* **23**:305-315.

Ray, D.E., Roubicek, C.B., Lane, A., Theurer, C.B. and McGinty, D.D. (1973) Supplementation or early-weaning with beef heifers. *J.Anim.Sci.* **36**:1203 (Abstr.)

Rege, J.E.O. and Moyo, S. (1993) Effect of birth date on growth performance of calves of seasonally-bred range cattle. *J.Anim.Breed.Genet.* **110**:209-227.

Reid, R.L. (1990) The Manual of Australian Agriculture. Sydney:Butterworths.

Reynolds, W.L., Bellows, R.A., Urich, J.J. and Knapp, B.W. (1986) Crossing beef x beef and beef x Brown Swiss : Pregnancy rate, calf survival, weaning age and rate. *J.Anim.Sci.* **63**:8-16.

Reynolds, W.L., De Rouen, T.M., Moin, S. and Koonce, K.L. (1979) Factors affecting pregnancy rate of Angus, Zebu and Zebu-cross cattle. *J.Anim.Sci.* **48**:1312-1321.

Richards, M.W., Spitzer, J.C. and Warner, M.B. (1986) Effect of varying levels of postpartum nutrition and body condition at calving on subsequent reproductive performance in beef cattle. *J.Anim.Sci.* **62**:300-306.

Richardson, F.D., Oliver, J. and Clarke, G.P.Y. (1975) Analysis of some factors which affect the productivity of beef cows and of their calves in a marginal rainfall ares of Rhodesia. 1. Factors affecting calving rate. *Anim.Prod.* **21**:41-49.

Richardson, F.D., Oliver, J. and Clarke, G.P.Y. (1977) Analysis of some factors which affect the productivity of beef cows and of their claves in a marginal rainfall area of Rhodesia. 2. The yield and composition of milk of suckling cows. *Anim.Prod.* **25**:359-372.

Roberts, S., Le Fever, D.G. and Wiltbank, J.N. (1970) Increasing reproductive efficiency in a cow herd. *J.Anim.Sci.* **30**:1032 (Abstr.)

Robinson, D.L. (1990) Genetic variances and covariances for liveweight in Queensland beef cattle. *Proc.Aust.Assoc.Anim.Breed.Genet.* **8**:435-438.

Robinson, D.L. and O'Rourke, P.K. (1992) Genetic parameters for liveweights of beef cattle in the tropics. *Aust.J.Agric.Res.* **43**:1297-1305.

Rollins, W.C. and Wagnon, K.A. (1956) Genetic analysis of weaning weights in a range beef herd operated under optimum and sub-optimum nutritional regimes. *J.Anim.Sci.* **15**:125-133.

Rudder, T.H., Burrow, H., Seifert, G.W. and Maynard, P.J. (1982a) The effects of year of birth, dam age, breeding and dam reproductive efficiency on liveweights and age at sale of commercially managed steers in central Queensland. *Proc.Aust.Soc.Anim.Prod.* **14**:281-284.

Rudder, T.H. and McCamley, K.D. (1972) A seasonal mating system for beef cattle in central Queensland. *Proc.Aust.Soc.Anim.Prod.* **9**:153-158.

Rudder, T.H., Seifert, G.W. and Bean, K.G. (1975) Growth performance of Brahman and Charolais x Brahman cattle in a tropical environment. *Aust.J.Exp.Agric.Anim.Husb.* **15**:156-158.

Rudder, T.H., Seifert, G.W. and Burrow, H.M. (1985) Environmental and genotype effects on fertility in a commercial beef herd in central Queensland. *Aust.J.Exp.Agric.* **25**:489-496.

Rudder, T.H., Tierney, T.J. and Maynard, P.J. (1982b) Factors affecting breeder herd productivity. *Proc.Aust.Soc.Anim.Prod.* **14**:211-213.

Rutledge, J.J., Robinson, O.W., Ahlschwede, W.T. and Legetes, J.E. (1971) Milk yield and its influence on 205-day weight of beef calves. *J.Anim.Sci.* 33:563-567.

Schneeberger, M. (1992) The alternative evaluation procedures. In:*Animal Breeding:The Modern Approach.* Eds. K. Hammond, H-U. Graser and C.A. McDonald. Post.Grad.Foundation in Vet.Sci., University of Sydney, p. 57-70.

Schneeberger, M., Tier, B. and Hammond, K. (1991) Introducing the third generation of Breedplan and Group Breedplan. *Proc.Aust.Assoc.Anim.Breed.Genet.* **9**:194-199.

Schillo, K.K., Hall, J.B. and Hileman, S.M. (1992) Effects of nutrition and season on the onset of puberty in the beef heifer. *J.Anim.Sci.* **70**:3994-4005.

Schlink, A.C., Gibson, D.S., Liang, Z.J. and Dixon, R. (1988) Calf management strategies and reproductive performance in a northern Australia cattle herd. *Proc.Aust.Soc.Anim.Prod.* **17**:326-329.

Schlink, A.C., Houston, E.M., Day, A. and Entwistle, K.W. (1994) Supplementation of *Bos indicus* cross calves grazing wet season tropical pastures. *Proc.Aust.Soc.Anim.Prod.* **20**:104-107.

Seebeck, R.M. (1973) Sources of variation in the fertility of a herd of Zebu, British and Zebu x British cattle in northern Australia. *J.Anim.Sci.(Camb)* **81**:253-262.

Seebeck, J.A. and Seebeck, R.M. (1982) Birth weights of different generations of Herefords and Shorthorn crosses. *Proc.Aust.Assoc.Anim.Breed.Genet.* **14**:88-89.

Seifert, G.W. (1971) Ecto- and endoparasitic effects on the growth rates of zebu crossbred and British cattle in the field. *Aust.J.Agric.Res.* **22**:839-850.

Seifert, G.W. (1975) Effectiveness of selection for growth rate in zebu x British crossbred cattle. I. Preweaning growth. *Aust.J.Agric.Res.* **26**:393-406.

Seifert, G.W., Corlis, P.L. and Rudder, T.H. (1980) The influence of dam age on weight for age of steers at weaning and after weaning. *Proc.Aust.Soc.Anim.Prod.* **13**:373-376.

Seifert, G.W., Rudder, T.H. and Lapworth, J.W. (1974) Factors affecting weaning weight of beef cattle in a tropical environment. *Aust.J.Exp.Agric.Anim.Husb.* **14**:277-280.

Setshwaelo, L.L. (1990) Beef cattle breeding in the tropics. *Proc.4th World Cong.Genet.App.Livest.Prod.* **XIV**:349-359.

Shepherd, R.K. (1986) Selection of statistical models for reproductive data. *Proc.Aust.Soc.Anim.Prod.* **16**:72-74.

Short, R.E. and Bellows, R.A. (1971) Relationships among weight gains, age at puberty and reproductive performance in heifers. *J.Anim.Sci.* **32**:127-131.

Short, R.E., Bellows, R.A., Moody, E.L. and Howland, B.E. (1972) Effects of suckling and mastectomy on bovine postpartum reproduction. *J.Anim.Sci.* **34**:70-74.

Sivarajasingam, S., Tier, B:, Robinson, D.L., Schneeberger, M. and Hammond, K. (1991) Improving the efficiency of removing environmental differences in EBV predicitions. *Proc.Aust.Assoc.Anim.Breed.Genet.* **9**:236-238.

Smith, B.A., Brinks, J.S. and Richardson, G.V. (1989) Estimation of genetic parameters among reproductive and growth traits in yearling heifers. *J.Anim.Sci.* **67**:2886-2891.

Smith, R.J. and Hearnshaw, H. (1981) Brahman bulls and dystokia problems. Agnote - New South Wales Department of Agriculture; **No.17/81**.

Srinivasan, G. and Martin, T.G. (1970) Environmental effects on preweaning performance of calves. *J.Anim.Sci.* **31**:168 (Abstr.)

Steenkamp, J.D.G., van der Horst, C. and Andrew, M.J.A. (1975) Reconception in grade and pedigree Africander cows of different sizes. I. Postpartum factors influence reconception. *S.Afr.J.Anim.Sci.* **5**:103-110.

Stricker, J.A., Matches, A.G., Thompson, G.B., Jacobs, V.E., Martz, F.A., Wheaton, H.N., Currence, H.D. and Krause, G.F. (1979) Cow-calf production on tall Fescue-Ladino clover pastures with and without nitrogen fertilisation or creep feeding:Spring calves. *J.Anim.Sci.* **48**:13-25.

Swanson, L.V. (1989) Discussion - Interactions of nutrition and reproduction. *J.Dairy Sci.* **72**:805-814.

Tawah, C.L., Mbah, D.A., Rege, J.E.D. and Oumate, H. (1993) Genetic evaluation of birth and weaning weight of Gudali and two-breed synthetic Wakwa beef cattle populations under selection in Cameroon : genetic and phenotypic parameters. *Anim.Prod.* **57**:73-79.

Taylor, J.F., Ladds, P.W. and Goddard, M.E. (1991) Carcass weights of cattle in relation to breed, sex, age, region of origin and season. *Aust.J.Exp.Agric.* **31**:745-752.

Taylor, W.J. and Rudder, T.H. (1984) The effect of mating replacement heifers as yearlings and two year old on herd output and structure. *Proc.Aust.Soc.Anim.Prod.* **15**:620-623.

Thompson, R. (1989) Design of experiments to estimate genetic parameters within populations. In : *Evolution and Animal Breeding*. Eds. W.G. Hill and T.F.C. Mackay. Wallingford, England:CAB International.p.169-174.

Thorpe, W., Cruickshank, D.K.R. and Thomspon, R. (1981) Genetic and environmental influences on beef cattle production in Zambia. 4. Weaner production from purebred and reciprocally crossbred dams. *Anim.Prod.* **33**:165-177.

Tier, B., Schneeberger, M., Hammond, K. and Fuchs, W. (1991) Determining the accuracy of estimated breeding values in multiple trait animal models. *Proc.Aust.Assoc.Anim.Breed.Genet.* **9**:239-242.

Topps, J.H. (1977) The relationship between reproduction and undernutrition in beef cattle. *World Rev.Anim.Prod.* **XIII**:43-49.

Trail, J.C.M., Buck, N.G., Light, D., Rennie, T.W., Rutherford, A., Miller, M., Pratchett, D. and Capper, B.S. (1977) Productivity of Africander, Tswana, Tuli and crossbred beef cattle in Botswana. *Anim.Prod.* **24**:57-62.

Tuen, A.A., Hodge, P.B., Smith, P.C., Day, P. and Murray, R.M. (1982) Mineral supplementation of *Bos indicus* cross cattle grazing native pastures in tropical Queensland. *Proc.Aust.Soc.Anim.Prod.* **14**:317-320.

Turner, H.A. and Farnsworth, G.L. (1993) Effects of reducing dystocia on heifer productivity. *Proc.West Sect., Amer.Soc.Anim.Sci.* **44**:336-339.

van Raden, P.M. (1990) Potential improvement in animal model evaluating systems. *Proc.4th World Cong.Genet.Appl.Livest.Prod.* **XIII**:357-363.

Vernon, E.H., Harvey, W.R. and Warwick, E.J. (1964) Factors affecting weight and score of crossbred-type calves. *J.Anim.Sci.* **23**:21-27.

Vesely, J.A. and Robinson, O.W. (1972) Empirical selection indexes for beef cattle. *J.Anim.Sci.* **34**:549-554.

Voh, A.A.Jr. and Otchere, E.D. (1989) Reproductive performance of zebu cattle under traditional agropastoral management in northern Nigeria. *Anim.Reprod.Sci.* **19**:191-203.

Waldron, D.F., Morris, C.A., Baker, R.L. and Johnson, D.L. (1993) Maternal effects for growth traits in beef cattle. *Livest.Prod.Sci.* **34**:57-70.

Warnick, A.C., Kirst, R.C., Burns, W.C. and Koger, M. (1967) Factors influencing pregnancy in beef heifers. *J.Anim.Sci.* **26**:231 (Abstr.)

Webster, C.C. and Wilson, P.N. (1980) Agriculture in the Tropics. (2nd)London:Longman.

Wettemann, R.P., Turman, E.J., Wyatt, J.D. and Totusek, R. (1978) Influence of suckling intensity on reproductive performance of range cows. *J.Anim.Sci.* **47**:342-346.

Wheat, J.D. (1970) Season variation in weights of Nigerian cattle. *J.Anim.Sci.* **31**:179 (Abstr.)

Whythes, J.R., Strachan, R.T. and Durand, M.R.E. (1976) A survey of dystocia in beef cattle in southern Queensland. *Aust.Vet.J.* **52**:570-574.

Willham, R.L. (1972) Beef milk production for maximum efficiency. *J.Anim.Sci.* **34**:864-869.

Williams, A.R., Franke, D.E., Saxton, A.M. and Turner, J.W. (1990) Two-, three- and four-breed rotational crossbreeding of beef cattle : reproductive traits.*J.Anim.Sci.* **68**:1536-1546.

Wilson, R.T. (1985) Livestock production in central Mali : Reproductive aspects of sedentary cows. *Anim.Prod.* **9**:1-9.

Wiltbank, J.N., Warnick, E.J., Vernon, E.H. and Priode, B.M. (1961) Factors affecting net calf crop in beef cattle. *J.Anim.Sci.* **20**:409-415.

Winks, L., Laing, A.R. and Stokoe, J. (1972) Level of urea for grazing yearling cattle during the dry season in tropical Queensland. *Proc.Aust.Soc.Anim.Prod.* **9**:258-261.

Winroth, H. (1990) Effect of non-genetic factors and development of adjustment factors for liveweight at different ages in beef herds. *Proc.4th World Cong.Genet.Appl.Livest.Prod.* XV:299-302.

Wray, N.R., Simm, G., Thompson, R. and Bryan, J. (1991) Application of BLUP in beef breeding programs. *British Cattle Breeders Club Digest* **46**:29-39.

Young (1968) Breeding patterns in commercial beef herds. 1. Herd performance in New South Wales. *Aust.Vet.J.* **44**:350-356.

APPENDIX

GLOSSARY OF TERMS

N	Number of observations
HS	F_n Hereford-Shorthorn cross
BX	F_n Brahman x Hereford-Shorthorn cross
BL	Brahman low grade
BH	Brahman high grade
AGEPLS	Cow age and previous lactational status
BWT	Birth weight
WWT	Age adjusted weaning weight at 200 days
YWT	Age adjusted yearling weight at 365 days
FWT	Age adjusted final weight at 550 days
CBDAY	Calf day of birth
HBDAY	Heifer day of birth
DAYOC	Day of calving
IWT	Cow liveweight at the start of the breeding season
MWGD	Cow weight gain per day during the breeding season