On farm

Final Report on Belmont Crossbreeding Project

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1. ABSTRACT

A crossbreeding study involving various breeds of African, Indian and European origins was conducted during 1992 – 1997 in tropical conditions of low to moderate parasite challenge to study the performance of various breed crosses and to quantify the heterotic advantage in crosses based on growth, adaptive, fertility, survival and meat quality traits. Zebu and Continental crosses excelled in growth traits and Zebu and its crosses had a clear advantage in adaptive traits. Heterosis estimates were high and significant in taurine – indicine crosses with British (tropically adapted Hereford-Shorthorn) – Zebu crosses showing highest heterosis among F_1s. Treatment to control ticks and worms resulted in significant weight gains in most of the taurine crosses under study but this is unlikely to be an economically viable and environmentally friendly option. Crossbred advantages are evident in fertility and survival traits as well, although of lower magnitude. Tenderness in predominantly Brahman herds of northern Australia can be improved through crossbreeding with taurine breeds. The crossbreeding parameters obtained from the present study can be used in either developing decision support tools for systematic crossbreeding or to optimise breed proportions in tropical composites.

2. EXECUTIVE SUMMARY

Tropical beef cattle in northern Australia face numerous challenges such as parasite infestation, hot climatic conditions and seasonal nutrition. To make this industry economically viable and environmentally friendly, it is essential to breed cattle that are fast growing, highly fertile, parasite and heat resistant. But to maintain the long-term sustainability and profitability of northern Australian beef cattle industry in the face of environmental concerns against use of chemicals to control parasites and competition from other livestock products, productivity must be increased with minimum input.

Productivity is a complex trait in northern Australian beef herds and encompasses components such as growth, tropical adaptation, and fertility and survival traits. No one breed excels in all the bioeconomic traits influencing the profit function in any livestock production system, more so in beef cattle as proven by many studies across various environments. Crossbreeding is one of the most useful tools to improve the performance of various bioeconomic traits by exploiting high levels of heterosis or hybrid vigour. However optimising the suitable crossbreeding system for any particular environment – market – management specifications depends on an understanding of the differences in performance of various breeds as heterosis depends on the genetic distance between contributing breeds in the traits of interest. This crossbreeding study outlines the differential performance of various breeds of African, European and Indian origins in harsh tropical environments and quantifies the heterotic advantage gained through crossing breeds of distinctly different genetic background. This experiment was conducted during 1992 – 1997. Various crosses were pooled together into 31 genotypes derived from tropically adapted British (B), Sanga derived (S), Zebu cross (Zx), Zebu (Z) and Continental (C) beef cattle breed groups to compare their performance based on growth, adaptation, temperament, fertility, survival and carcass and meat quality traits. British cattle in this study were the Belmont Adaptaur (Hereford-Shorthorn cross), which is a tropically adapted line selected for tick resistance and 550-day liveweight. Hence it does not represent temperate British breeds. Belmont Red and Tuli constituted Sanga derived breeds and Brahman and Boran were grouped under Zebu. Charolais and Simmental constituted the sire breeds of Continental origin. Female fertility and calf survival traits were analysed as traits of the dam to study the differences in the parental breeds.

Major results from the study are:

Growth traits

Breed differences were significant and in general, crossbred calves performed significantly better than purebred calves. Calves out of Zebu dam breeds had lower birth weights, and Zebu sire breeds and Sanga derived dam breeds resulted in heavier birth weights. ZC (Zebu dam crossed with Continental sire), and ZC cross with Sanga and Zebu sires had heavier weights and higher weight gains until 18 months of age. Direct breed additive effects of C, Z and S expressed as a deviation from the British mean were high and significant for all the growth traits indicating their better realised growth than the British in this environment. The magnitude of dominance effects, causing heterosis, was higher in taurine x indicine crosses e.g., Brahman cows x Belmont Adaptaur bulls, indicating the advantage of *Bos taurus x Bos indicus* crosses. Taurine x indicine crossbred dams provided the best maternal environment resulting in crossbred dams rearing bigger calves. The crossbreeding parameters estimated for growth traits are useful in developing prediction models for predicting the performance of untested genotypes in similar environments. The percent heterosis estimates were highest in Zebu x British crosses for growth traits (8 to 19%).

Adaptive traits and temperament

Zebu and its crosses had better parasite and heat resistance than taurine crosses. No clear breed differences were noticed in flight time, a measure of temperament. The better adaptability of Zebu and its crosses was evidenced by the significantly negative (favourable) breed additive component in all adaptive traits relative to the British. Sanga derived and tropically adapted British breeds had similar tick resistance but Sanga derived breeds had lower worm resistance than the British as evidenced by the additive genetic components. Continental breed group tick resistance levels were also lower than the British. Tick, worm and heat resistance levels increased in crossbreds especially in taurine x indicine crosses due to the significant and favourable dominance effects. High and significant heterosis percentages were observed in Zebu x British crosses for all the adaptive traits. Favourable and significant heterosis percentages were also observed in Sanga x British crosses for tick resistance.

Treatment to control ticks and worms significantly increased postweaning live weight gains in many genotypes. As the *Bos indicus* proportion in the genotype increased, the response to treatment in live weight gain reduced. Taking into consideration the economic cost it is prudent to breed parasite resistant taurine – indicine crosses rather than to treat against ticks and worms.

Fertility and survival traits

High scrotal circumference in British bulls and taurine crossbreds (British x Sanga) as opposed to Zebu and its crosses was noticed indicating potentially good semen characteristics and seminal volume of British bulls. Most of the heterosis in scrotal circumference was due to the heterosis in body weight. Heterosis estimates were not significant when scrotal circumference was adjusted for body weight. Among purebreds, calving success was high in Belmont Adaptaur wet (lactating) cows and high in Brahman and Brahman cross in dry (non-lactating) cows and heifers. There was no concrete evidence of low fertility of Brahmans from the present study. In general, crossbreds had better calving success than purebreds especially in dry cows and heifers. There was also an advantage of crossbred dams over purebred dams in days to calving. Even though there was a crossbred advantage in fertility traits, heterosis was generally low and insignificant except in crosses between Brahman and Belmont Red.

Preweaning calf survival proportions of crossbred dams were in general higher than those of the purebred dams. High mortalities in calves born to British dams from Zebu sires were noticed indicating the incidence of dystocia. Low and insignificant heterosis was observed in survival traits.

Carcass quality traits

The major observation of the results from carcass quality traits was that the tenderness of grilling and roasting cuts of meat from the predominantly Brahman-based beef herd of northern Australia can be improved through crossbreeding with taurine breeds. There was no evidence of heterosis in any eating quality attribute. For both feedlot finished and pasture finished steers, striploin steaks from British steers were most tender, and Sanga and Zebu x Continental cross steaks were more tender than Zebu steaks. Evidence existed for a Brahman sire whose progeny had both high marbling scores and intra muscular fat. This signifies the possibility of farming tropically adapted high marbling crossbreds or composites targeting markets preferring high marbling.

Knowledge of performance of various breed crosses and the parameter estimates obtained from this study can be used to develop models for predicting the performance of untested genotypes in similar environments. They are also useful in deriving the optimal breed proportions in tropical beef composites. With the diversified target markets available for beef cattle trade, the importance of development of composites that can perform well under tropical conditions is ever growing. So to address such specific requirements, precision in the design of breeding programmes is crucial. This can be realised through the development of decision support software which can utilise the parameters obtained from this study and from other published literature and combine it with the economic weightings needed for various traits under different environments. Besides helping in the development of these precise prediction models, the present study also allows us to draw some simple conclusions such as the higher benefits through heterosis from crossing taurine and indicine breeds as opposed to maintaining a single breed stock. Crossbreeding also helps to improve the traits that are not influenced by heterosis, such as meat quality characteristics, by producing genotypes that perform at an average value of the parental breeds.

3. MAIN RESEARCH REPORT

3.1. Background of the study

Crossbreeding has evolved as an efficient breeding tool to improve productivity in tropical regions of Australia. The need to combine parasite and heat resistance traits with high growth rates and good meat quality attributes has provided an economic incentive for crossbreeding. At a genetic level, crossbreeding systems provide a means to utilize both additive and non-additive gene action simultaneously. There are many studies on crossbreeding in temperate regions (e.g. Long 1980, Gregory and Cundiff 1980), but research on crossbreeding in tropical climates is limited.

Because of well established genotype x environment interactions in comparative growth rates (Frisch and Vercoe 1984; Arthur *et al.* 1994*a*) of various breeds, results obtained in one environment with a particular set of breeds cannot be generalised for all the environments. Moreover, in tropical environments, stressors like high humidity and temperature, ecto- and endo-parasites, disease incidence, and seasonal nutrition affect the growth performance of various genotypes. Hence, growth in beef cattle in a tropical environment is influenced by their genetic potential for growth and their adaptation to environmental stressors like ticks, worms and high temperature and humidity. In the extensive pastoral regions of Australia, the use of breeds that have inherently high parasite resistance makes sound economic sense, particularly because parasite control using chemicals is not feasible in most of these areas. Parasites acquiring resistance to the chemicals used to treat them compound these problems. The increasing awareness of chemical residues in meat and milk further necessitates the need to look for alternate strategies to control external and internal parasites in beef cattle. One of the most economic and easy solutions is to farm cattle that are resistant to the parasites. Crossbreeding can be used as a breeding tool to combine the traits of economic importance like growth, parasite and heat resistance in the resulting crosses.

Reproductive or fertility traits have the highest impact on the profitability of a beef cattle enterprise, in that a unit increase in genetic gain obtained in fertility influences the profit function to a greater extent. However, these traits are difficult to measure, analyse and interpret more so, in pasture based mating systems. The improvements in fertility traits can only be realised as profits when there is a simultaneous improvement in calf survivals especially before weaning. Hence, it is important to study the fertility and survival traits of various breeds and their crosses in the harsh tropical climate so that wise breeding decisions can be made. With this background, a crossbreeding experiment involving various African, Indian and European beef cattle breeds with various levels of tropical adaptation was conducted with the following objectives. While the main objectives are the much broader aims / goals of the project at the conception level, work objectives are the objectives used to achieve these broader goals.

3.2. Objectives of the study

3.2.1. Main objectives

1. To identify the most productive genotypes for any given set of market-management-environment conditions in northern Australia.

2. Produce models that will allow the prediction of productivity of any given genotype for any defined set of market-management-environment conditions.

3.2.2. Work objectives

1. To compare the performance of various breeds and their crosses in a tropical environment with low to medium parasite challenge for differences in growth traits.

2. To estimate genetic effects of growth traits that allows the prediction of performance of untested genotypes thereby helping the better design of a crossbreeding programme.

3. To compare the tick counts, worm egg counts, rectal temperatures, coat scores, buffalo fly scores and flight time of various genotypes derived from this crossbreeding experiment as a measure of their parasite and heat resistance and temperament.

4. To estimate direct and maternal genetic effects for the adaptive and temperament traits.

5. To study the effect of treatment to control ticks and worms on live weight gains.

6. To identify the breed / breed group differences in male fertility (scrotal circumference) and female fertility (calving success and days to calving) traits.

7. To identify the breed / breed group differences in calf survival at various ages.

8. To identify the breed group differences for meat and carcass quality attributes.

9. To optimise breed proportions of a tropically adapted beef composite utilising both growth and resistance traits.

3.3. Project outcomes

3.3.1. Growth traits

3.3.1.1. Breed pooling and data

Between 1992 and 1997, various breeds of African, European and Indian origin were crossed to compare various genotypes at the National Cattle Breeding Station, 'Belmont', near Rockhampton, Queensland, Australia. The station is located 25 km north of the tropic of Capricorn, 40 km from the coast. The climate is dry tropical with unreliable wet seasons, with two-thirds of rainfall occurring between December and March. Winter (June to August) is the "dry" period of low nutrition. Cattle are subjected to numerous environmental stressors like high temperatures and humidity during summer, nutritional deficiency during the "dry" season, ecto-parasites (*Boophilus microplus* and buffalo fly, *Haematobia irritans exigua*), endo-parasites (gastro-intestinal helminths or worms, predominantly *Haemonchus*, *Cooperia* and *Oesophagostomum* species), and periodic exposure to diseases (Bovine Infectious Kerato-conjunctivitis and Ephemeral fever). A total of 122 genotypes with the number of animals in each cross ranging from 1 to 338 were produced between 1992 and 1997. Only 71 genotypes that had at least 10 progeny / genotype were included in the present analysis. Breeds were further regrouped based on their origins and similarities (Table 1) producing 31 genotypes for evaluation (Table 2). Belmont Adaptaur (HS), Belmont Red (AX), and Belmont BX (BX) are the synthetic breeds developed at Belmont by crossing and *inter se* mating for several generations to stabilise respective breed proportions in these lines (Frisch and O'Neill 1998*a*).

Table 1. Breed group formation from the breeds involved in the study

Breed group name	Dam breeds	Sire / Sire of the dam breeds
	Bos taurus derived	
Tropically adapted British (B)	Belmont Adaptaur (HS) (Synthetic breed of ½ Hereford, ½ Shorthorn)	HS Shorthorn*
Sanga derived (S)	Belmont Red (AX) (Synthetic breed of ½ Africander, ¼ Hereford, ¼ Shorthorn)	AX, Tuli (Tu)
Continental (C)		Charolais (Ch), Simmental (Si)
	Bos indicus derived	
Zebu (Z)	Brahman (Bh)	Brahman (Bh), Boran (Bo)
Zebu cross (Zx)	Belmont BX (BX) (Synthetic breed of ½ Brahman, ¼ Hereford, ¼ Shorthorn)	BX

*Only represented as sire breed of crossbred dams

The grouping of Brahman and Boran together was based on their similarities and closeness as indicated in earlier studies on those populations (Frisch *et al.* 1997; Frisch and O'Neill 1998*a*). Tuli was grouped with Belmont Red because of their common Sanga *taurus* constitution. Sanga derived group predominantly consisted of Belmont Red in the present study. British purebreds in this study were the Belmont Adaptaur (Table 1), which is a tropically adapted line selected for tick resistance and 550-day liveweight. In this report, B, S, Zx, Z, and C represent tropically adapted British, Sanga derived, Zebu cross, Zebu, and Continental breed groups respectively (Table 1). In crosses, the female parent is shown first with crossbred dams and sires shown in parentheses. Purebred performance information was not available for Boran, Tuli, Shorthorn, Charolais, or Simmental as they were only represented in crosses. Hence, ZZ represented only Brahman and Brahman x Boran cross, SS represented predominantly Belmont Red and a few Belmont Red x Tuli cross, and BB represented only Belmont Adaptaur. Shorthorns were only represented as sire breed of the crossbred dams. BB, SS, ZxZx and ZZ were grouped as purebreds and from F_1 back cross onwards (Table 2) reciprocals within dam breed group were pooled together.

Live weights were recorded at birth, weaning, yearling age, and around 18 months of age (hereafter referred to as final weight). Average weaning age, yearling age, and age at final weight were 193, 372, and 524 days respectively. Except during the 10-week breeding season, all cows grazed as a single herd. Up to weaning, none of the calves or their dams was treated to control endo- or ecto- parasites. All male calves remained entire until after final weight was recorded. Steers and heifers were managed as separate cohorts after weaning and calves from each crop were allocated randomly within sex, breed, sire and previous lactation status of the dam into either a treatment group or a control group. Animals in the treatment group were treated with anthelmintic to control gastrointestinal nematodes regularly every 3 weeks from around 8 months of age to around 18 months of age. They were also inspected for cattle ticks (*Boophilus microplus*) and if ticks were present, all the treatment group animals were dipped in a plunge dip containing acaricide (Tactic, Hoechst, Australia). AX, Bh and BX sires were selected for high 600 day live weight estimated breeding value and HS sires were selected for high 550 day live weight and high resistance to cattle ticks. Bo, Tu and Ch sires were selected at random. The focus was to increase the number of sires per breed rather than to increase number of progeny per sire as the study was intended to understand breed differences. Further details are presented by Prayaga (2003*a*, see appendix).

Animals with missing information on date of birth, disputed parentage, with no proper breed identification and those animals whose weights (outliers) were affected by lantana (*Lantana camara* L.) poisoning were removed from the analyses. After all the edits, 2608 animals with birth weight, 2556 animals with weaning weight, 2460 animals with yearling weight and 2440 animals with final weight records were used in the analysis. The number of animals in each breed group for each weight is given in Table 2.

3.3.1.2. Statistical analyses

Data pertaining to birth weight, weaning weight, average daily gain (ADG) from birth to weaning, yearling weight, final weight, and postweaning ADG (ADG from weaning to final weight) were analysed using a univariate fixed effects model (model 1) in ASREML (Gilmour *et al.* 2001). Model 1 included the effects of genotype, contemporary group (consisting of year of birth, season of birth and age of dam), sex, and treatment (only for traits after weaning), and previous lactation status of the dam. Year of birth ranged from 1991 to 1996 and months of birth were regrouped into 3 seasons (August – September, October – November and December – January). Age of dam at the time of calving was grouped into 3, 4, 5 and ≥ 6 years. Previous lactation status of the dam was categorised as wet (lactating) cow, dry (non-lactating) cow, cow with a dead calf and maiden heifer. Weaning weight, yearling weight, and final weight were adjusted for respective ages at the time of weighing by including age at weighing as a covariate. After testing the possible first order interactions for significance, all significant interaction effects were included in the analysis.

Genetic effects or the crossbreeding parameters for various growth traits were estimated using a multiple regression approach using the fractional coefficients of genetic effects for various genotypes included in the study. A detailed description of the procedure of estimation and the table showing the fractional coefficients of genetic effects are presented by Prayaga (2003*a*, see Appendix). Breed groups were regrouped as *Bos taurus* (B, S, and C) and *Bos indicus* (Z, Zx), as shown in Table 1, for the estimation of dominance effects thereby dividing the crosses into taurine-taurine (TT), taurine-indicine (TI) and indicine-indicine (II) crosses. Heterosis estimates were only derived for those F_1 crosses where reciprocals existed. Heterosis was estimated using least squares means for each trait as a deviation of the F_1 mean from the parental population mean and expressed as a percentage of the parental population mean.

3.3.1.3. Results and Discussion

3.3.1.3.1. Genotype differences

The main purpose of crossbreeding in a tropical environment is to improve the performance of animals under stressful environmental conditions by complementing the desirable genes from both parental breeds. Significant genotype differences in the present study emphasise the need for proper selection of breeds in crossbreeding programmes by taking into consideration genetic complementarity of sire and dam breeds and environmental adaptation of the resulting genotype. Least squares means for various growth traits in various genotypes are presented in Table 2. The overall mean birth weight was 33.7 kg (range 29.4 to 38.1 kg) with male calves weighing 2.4 kg more than females. Z (Zebu) dam breeds produced calves with the lightest birth weights and S (Sanga) dam breeds resulted in the heaviest birth weights. Low birth weights of Zebu straightbreds as well as relatively low birth weights in crosses where Zebu breed was used as a dam reinforces the view that Brahman (Roberson *et al.* 1986) and Boran (Frisch and O'Neill 1998*a*) dams produce smaller calves. Hence, in stressful tropical conditions where lower birth weights may be desirable for calving ease, Z breeds are better suited as dam breeds. When Z was used as a sire breed rather than a dam breed, birth weights increased. Within F_1s, Zebu dams had calves with lower birth weight except in ZC (Zebu dam cross with Continental sire). Birth weights were generally heavier wherever ZC was used as either a dam or sire. As heavier birth weights are associated with production problems (dystocia, calf loss, reduced calf performance) for beef producers and as there are no significant complications associated with medium birth weights in the range indicated by these results, cross breeding programmes should be aiming to maintain medium birth weight ranges.

The overall mean weaning weight was 194 kg (range 157 to 216 kg) and male calves were 17 kg heavier than female calves. Mean preweaning ADG was 832 g/day (649 to 938 g/day) with males gaining 75 g/day more than females. Ranking of breed groups changed significantly at weaning relative to their ranking at birth. Changes in rankings of genotypes in weaning weight and preweaning ADG relative to birth weights are attributed to differences in maternal abilities of dam breed groups and differences in expression of additive genetic potential of calves under stressful climatic conditions. ZC (Zebu dam cross with Continental sire) and ZC crosses with S and Z were significantly heavier at weaning and had higher preweaning ADG. This reflects the heavier mature size of Continental breeds contributing to heavier weaning weights and faster daily gains in their progeny compared to other taurine breeds used in the study. BB (Belmont Adaptaur) was the lightest at weaning and had the lowest preweaning ADG. Lower weaning weights and preweaning ADG observed in calves from the British dams can be attributed to their low milk producing ability under tropical environments (Lamond 1973) and the relatively lower adaptation of calves to ticks, worms and heat. BZ and BS i.e., crossbred calves reared by British dams, also had low weaning weights and preweaning ADG. Calves reared by Zebu crossbred dams in F_1 backcrosses and three breed crosses performed well for preweaning growth traits.

The overall mean yearling weight was 226 kg (range 182 to 254 kg). The overall weight gain from weaning to yearling age was 32 kg (226 – 194 kg) over 179 days (difference between mean yearling and weaning ages) at around 176 g/day. In tropical and subtropical environments in Australia, this period between weaning to yearling age coincides with the traditional "dry" season and hence calves usually maintain their weaning weights or in some cases lose weight between weaning and yearling ages. The overall mean final weight was 324 kg (range 263 to 368 kg). The heaviest and the lightest genotypes at weaning (ZC and BB) ranked the same at final weight. C breed crosses with Z and S attained heavier weights than crosses involving British breeds. Among F_1s, BS and SB (100% *Bos taurus*) performed poorly. However BZ and ZB performed relatively better as they benefited from significant *Bos taurus* x *Bos indicus* heterosis. Better performance of 3-breed crosses and F_1 x F_1 crosses also reflected the expression of heterosis. The mean postweaning ADG over all genotypes was 394 g/day (range 319 to 459 g/day). ZC recorded the fastest postweaning ADG, followed by (ZZx)S. The slowest postweaning ADG was observed in the genotypes with the highest *Bos taurus* content (i.e., (ZxB)B, BB, BS, SB, and (ZB)B).

In the present study, conditions were not typical of normal tropical conditions. Lower parasite burdens and treatment of half of the animals against ticks and worms in the postweaning period boosted the overall performance of certain genotypes like ZC. The use of C breeds at higher proportions in crossbreds may improve the growth performance as shown in this study, but it may affect the overall productivity because of increased maintenance requirements due to heavier mature sizes. This is of concern when most or all of the heifer calves are to enter the breeding cowherd. However, if parasite resistance is also considered for breed selection in crossbreds, the proportion of continental breed in the crossbreds may be reduced (discussed later).

Table 2. Least squares means of pre and post weaning growth traits for various genotypes under study

Breed group in genotype as given in Table 1 with female breed given first in the crosses and crossbred dams and sires identified in parentheses, bwt – birth weight, wwt – weaning weight, ywt – yearling weight, fwt – final weight at 18 months, pre ADG – preweaning average daily gain, post ADG – postweaning average daily gain, N- number of records, Differences between means of >1.8 kg, >8.2 kg, >39.6 g/day, >10.2 kg, >12.5 kg and >26.3 g/day (based on overall standard error of difference) are significantly different for bwt, wwt, pre ADG, ywt, fwt and post ADG respectively.

Genotype	N	bwt (kg)	N	wwt (kg)	pre ADG (g/day)	N	ywt (kg)	N	fwt (kg)	post ADG (g/day)
Over all	2608	33.7	2556	194	832	2460	226	2440	324	394
Purebred										
BB	316	31.9	302	157	649	271	182	270	263	319
SS	231	36.3	225	188	786	221	221	217	316	388
ZxZx	58	31.5	56	184	793	52	215	50	312	384
ZZ	274	30.4	265	187	815	251	218	251	320	404
F_1										
BS	46	32.9	46	170	706	46	204	46	290	365
SB	22	36.7	21	182	750	20	214	20	297	354
BZ	92	36.7	92	178	733	89	219	87	322	436
ZB	116	30.7	114	195	849	110	233	108	334	423
SZ	137	38.1	137	196	822	131	233	131	339	432
ZS	179	31.3	176	199	870	169	236	164	342	433
ZZx	52	30.4	51	188	814	50	219	50	320	402
ZxZ	102	34.1	102	193	830	100	227	99	328	406
ZxS	58	31.4	56	193	839	52	224	52	323	391
ZC	93	34.4	92	216	938	90	254	90	368	459
F_1 backcross										
(ZB)B	56	32.1	56	196	844	56	221	56	313	355
(ZB)Z	120	35.4	120	203	867	118	231	118	325	369
(ZS)S	35	33.5	35	204	879	35	235	35	335	399
(ZS)Z	64	34.3	63	203	875	63	231	63	333	396
(ZZx)Z	21	32.1	20	194	833	18	226	17	327	418
(ZxB)B	49	33.4	49	186	792	49	205	48	291	318
(ZC)Z	43	36.8	42	213	911	42	242	42	344	403
3-breedcross										
(BS)Z	20	36.1	20	195	825	19	237	19	331	414
(ZB)S	116	33.7	114	206	892	112	232	111	330	375
(ZZx)S	35	32.8	34	195	840	35	238	35	340	441
(ZC)S	28	35.8	28	215	922	27	247	27	349	394
Z(BS)	41	29.4	39	190	836	39	222	39	324	407
S(ZC)	31	37.0	30	203	860	29	225	29	330	390
F_1 x F_1										
(ZB)(SZ)	49	33.4	46	200	860	44	233	44	329	388
(ZS)(SZ)	65	33.7	65	196	840	64	221	64	316	366
(ZS)(ZC)	33	34.5	33	204	881	32	230	32	332	391
(BS)(ZC)	26	34.7	26	193	816	26	225	26	325	405

3.3.1.3.2. Genetic effects

Genetic effects or crossbreeding parameters are essential for predicting the performance of untested genotypes in a given environment and they are crucial in designing any breeding programme involving crossbreeding. These breed genetic effects are additive and dominant in nature and each of them can either be direct or maternal. Direct additive effect refers to the relative direct advantage or disadvantage a breed passes on to the next generation for the trait of interest irrespective of it being used as dam or sire. Maternal additive effect refers to the relative advantage or disadvantage a breed passes on to the next generation if that breed was used as a dam breed. Direct dominance effects refer to the crossbreeding effects meaning the extra advantage or disadvantage progeny inherit from their parental breeds when two different breeds are crossed. The maternal dominance refers to the crossbred dam advantage or disadvantage over the purebred dam.

Direct and maternal genetic effects of various breed groups for growth traits are presented in Table 3. The direct (a) and maternal (m) breed additive effects were expressed as deviations from the tropically adapted British (BB) breed mean. The positive and significant breed additive effects of S, Zx, Z and C relative to the British mean emphasise the low realised growth of British (tropically adapted Belmont Adaptaur) in this environment. The Continental breed group has the greatest additive effect (aC) for all growth traits, followed by Zebu (aZ) and Sanga derived (aS) breed groups.

Table 3. Crossbreeding parameters for various growth traits of various breed groups in the study

a- breed additive, m – breed maternal, dD – direct dominance, mD – maternal dominance, II – indicine x indicine cross, TI – taurine x indicine cross, TT-taurine x taurine cross, S- Sanga, Zx- Zebu cross, Z – Zebu, C- Continental

	Birth weight (kg)	Weaning weight (kg)	Preweaning ADG (g/day)	Yearling Weight (kg)	Final Weight (kg)	Postweaning ADG (g/day)
Direct breed effect (direct additive)						
aS	2.0 **	16.4 **	72.7 **	24.5 **	36.5 **	59.8 **
aZx	1.7	7.8	28.6	13.4 *	27.9 **	63.8 **
aZ	4.0 **	16.0 **	63.4 **	24.0 **	42.1 **	82.6 **
aC	7.3 **	46.4 **	194.6 **	49.7 **	78.5 **	97.2 **
Dam breed effect (maternal additive)						
mS	1.4 *	9.9 **	46.7 **	6.5	6.8	-6.5
mZx	-3.1 **	14.7 **	95.8 **	10.2 *	8.5	-19.1
mZ	-5.8 **	13.3 **	97.8 **	10.2 **	10.7 **	-6.5
mC	1.5	4.3	16.4	7.8	3.9	-3.3
Crossbreeding effect (direct dominance)						
dD_{II}	1.5 **	5.8 **	24.0 *	8.6 **	11.0 **	14.5 *
dD_{TI}	1.7 **	11.4 **	49.7 **	17.9 **	26.2 **	44.8 **
dD_{TT}	0.2	6.2 **	28.0 *	5.7	7.1	4.9
Maternal crossbreeding effect (maternal dominance)						
mD_{II}	0.9	1.4	-1.7	8.7 *	6.4	20.4 *
mD_{TI}	1.1 **	15.7 **	73.1 **	9.9 **	7.1 **	-25.8 **
mD_{TT}	-1.5	5.8	36.3 *	8.4 *	4.5	-1.2

*$P<0.05$, **$P<0.01$

The general perception of the Brahman's contribution to commercial beef cattle production is their favourable maternal influence in early calf growth and their advantage in adaptation to tropical and subtropical environments (Roberson *et al.* 1986). The present study supports this perception as evidenced by very significant maternal additive effects of Z and Zx (dam breed effects mZ and mZx) for weaning weight and preweaning ADG. Significant and high mZ and mZx for weaning weight indicate greater maternal ability of dams in the Z and Zx breed groups, which in turn reflect their good milk producing ability. Reports of high milk production of Brahman and Brahman crosses in temperate (Cundiff *et al.* 1986) and tropical (Lamond 1973) environments support this inference.

For birth weight, breed maternal additive effects of Z (mZ) and Zx (mZx) were significant and negative explaining the lower birth weights of calves from Zebu dams. The lower birth weights obtained by purebred ZZ are due to the higher negative breed maternal effect (mZ) overriding the positive breed additive (aZ) effect. In the cross of B dams mated to Z sires, high direct breed additive effect of Z sires for birth weight and significant positive dominance effects caused an increase in birth weight, which led to an increase in the rate of calf mortality in British dam breeds. This increased calf mortality and dystocia in British dam breeds crossed to Zebu sires was noticed in the present study (given in later section on calf survivals). This combination of large positive direct breed additive and large negative breed maternal additive effects of Zebu breeds for birth weight can be exploited by careful design of breeding programmes depending on the need and environmental conditions.

Only mZ was significant up to final weight implying that in Zebu crosses, breed maternal effects are important even for final weight. Though breed maternal additive effects are only expected to be significant up to weaning, there may be some carry over effect to yearling weight. However, it would not be expected that they would persist to final weight. But in the case of Zebus, prolonged influence of maternal effects is observed in the present study.

Though Continental pure breeds were not tested for their performance in the present study, their performance is expected to be poor because of their lack of resistance to stressors of tropical environments similar to other taurine breeds (Frisch and O'Neill 1998*b*). However, because of their very large direct breed additive effect (aC) on growth, their crosses with Z dam breeds with 25 – 50% C breed group proportion perform well due to complementarity (Table 2).

Crossbreeding (direct dominance) effects were significant for all the traits in II (indicine x indicine) and TI (taurine x indicine) crosses, which indicated the presence of significant heterosis in the crosses under study. The magnitude of crossbreeding effects in TI crosses was more than double that of II crosses for all the traits, except birth weight. TT (taurine x taurine) crosses resulted in significant direct dominance effects only for weaning weight ($P<0.01$) and preweaning ADG ($P<0.05$). The significant direct dominance effects in the present study indicated the crossbred advantage over straightbreds. The lack of significance in direct dominance effects in crosses among taurine breeds for birth weight and postweaning growth traits is due to the genetic similarities among taurine breeds. Significant and high direct and maternal dominance effects in TI crosses emphasised that hybrid vigour was better exploited by crossing the breeds of most distant relationship such as taurine and indicine origins. Cundiff *et al.* (1986) also demonstrated the significant contribution of *Bos indicus* breeds in temperate climates through crossbreeding, as the heterosis for growth traits was greatest for *Bos taurus* x *Bos indicus* crosses. Franke *et al.* (2001) reported significant direct heterosis effects for Brahman x Charolais and Brahman x Hereford crosses for birth weight, average daily gain and 205 day weight in a subtropical environment of USA and stated that these heterosis effects were significantly greater than those not including Brahman in the cross. This is comparable to high and significant crossbreeding effects in TI crosses in the present study.

Crossbred dam (maternal dominance) effects were only significant ($P<0.01$) in TI crosses for all growth traits under study. These results reflect the importance of breed selection in maternal lines to exploit maternal heterosis. The positive and significant mD_{TI} for weaning weight and preweaning ADG in the present study indicates that taurine x indicine crossbred dams provide better maternal environment to their calves than purebred or taurine crossbred or indicine crossbred dams. These mD_{TI} effects are in agreement with Roberson *et al.* (1986) and Arthur *et al.* (1994*b*) and refer to the improved performance in progeny by using crossbred rather than purebred dams.

The significant and positive mD_{II} effect on postweaning ADG indicates that indicine crossbred dams have a positive effect on postweaning growth rate of their calves. Compensatory growth (Arthur *et al.* 1994*b*) observed in postweaning periods in crosses where there was slow preweaning growth rate could be the reason for the progeny of II crosses having high maternal dominance effect for postweaning ADG. However, because of lower direct dominance effects in II crosses compared to TI, the overall performance of progeny resulting from II (indicine x indicine) crosses will be lower than TI (taurine x indicine) crosses.

These results suggest that a dam line of indicine crosses (for e.g. Brahman x Boran cross) or taurine indicine cross (for e.g. Brahman x Belmont Red cross) mated to taurine sire breeds (for e.g. Charolais) may result in fast growing progeny because of the optimum exploitation of additive and non-additive genetic effects for growth traits in this environment. However, respective proportions in the resulting cross and the breeding programme again depend on the climatic conditions (sub-tropical or tropical) and parasite challenge (low or high tick and worm infestation). Also, the inclusion of traits such as fertility in the model for evaluation may affect this conclusion. Importantly, the genetic effects derived in this analysis are specific to this tropical environment with low parasite load. Extrapolation and prediction of performance of any breed from these crossbreeding parameters, for e.g. purebred performance of Charolais in tropical climates would lead to wrong predictions. However, if the parameters are not available for any specific environment different to that discussed in the present study, inclusion of general rules of thumb such as the 25% tropically adapted genes in subtropical climates and up to 50% tropically adapted genes in tropical environments may allow these parameters to apply universally for prediction of growth performance.

3.3.1.3.3. Heterosis

Bos indicus cattle are better adapted and more resistant to ticks and worms (Frisch and O'Neill 1998*b*), while *Bos taurus* cattle have higher growth rates in less stressful environments (Arthur *et al.* 1994*a*). Crosses between these distinctly different breed groups result in hybrid vigour for growth and adaptive traits such as resistance to ticks and worms. Percent heterosis for selected two breed group crosses (F_1s), where reciprocals existed, are presented in Table 4. Heterosis percentages were positive in all crosses. The percent heterosis values ranged from 2.1 to 8.2% for birth weight, 2.2 to 8.5% for weaning weight, 1.5 to 8.0 % for preweaning ADG, 2.8 to 13.1% for yearling weight, 1.3 to 12.7 % for final weight and 1.7 to 18.8 % for postweaning ADG. In beef cattle, direct heterosis effects generally range from 1 to 11% for birth weight, 3 to 16% for weaning weight, 3 to 8% for preweaning ADG, 2 to 7% for yearling weight, 1 to 8% for post-yearling weight and 2 to 11% for postweaning ADG (Long, 1980). The present estimates of direct heterosis percentages fall in this range. Higher heterosis estimates were observed for the postweaning growth traits in Z and B crosses in the present study. This substantiated the earlier conclusion that when tropically adapted genes (Zebu) were present at around 50% level in tropical environments, the high crossbreeding effects would influence growth by overriding the low additive and maternal genetic effects of one of the parental breeds.

Table 4. Percentage heterosis (%) in selected F_1 genotypes (where reciprocal crosses were available) for various growth traits

Genotype as shown in Tables 1 and 2

Genotype	Birth weight	Weaning Weight	Preweaning ADG	Yearling weight	Final weight	Postweaning ADG
SB / BS	2.1	2.2	1.5	3.8	1.3	1.7
ZB / BZ	8.2**	8.5**	8.0**	13.1**	12.7**	18.8**
ZS / SZ	4.0	5.4*	5.7*	7.0**	7.2**	9.2**
ZZx / ZxZ	4.2	2.5	2.2	2.8	2.6	2.5

*P<0.05, **P<0.01

3.3.2. Adaptive and temperament traits

3.3.2.1. Data

Breeds and management for adaptive traits were the same as those, which applied to growth traits (3.3.1.1). The abbreviations and definitions of the traits recorded are shown in Table 5 and number of animals and records in each trait are given in Table 6. TICK and EPG were recorded on all weaned animals over a nine-week period at three weekly intervals before commencement of the treatment. After this period, from around 8 months of age, TICK and EPG were recorded on control animals at various postweaning ages until 18 months of age. Data editing of TICK was based on the mean tick counts and the number of zero counts in each of the year – count number sub classes. If the number of zeros in any of these sub-classes was more than 25% and mean tick count was <10, the data from that particular subclass was omitted from analyses because it was deemed that insufficient challenge existed to determine an animal's resistance to ticks.

Table 5. Abbreviation and definition of the adaptive and temperament traits recorded

Trait	Definition
Adaptive traits	
TICK	Mean number of ticks recorded at various postweaning ages by counting the number of engorging ticks of ≥ 4.5 mm long on one side of the animal following field infestations (Wharton *et al.*, 1970).
EPG	Mean number of worm eggs per gram of faeces at various postweaning ages (Roberts and O'Sullivan 1950) as recorded by one experienced technician.
TEMP	Mean rectal temperatures of animals recorded at various postweaning ages during summer months when the ambient temperatures were > 30^0C.
COAT	Mean coat scores of animals averaged over various postweaning scores. The scoring system was subjective and ranged between 1 (extremely short and sleek coat) to 7 (very woolly coat) as described by Turner and Schleger (1960).
Temperament	
FT	Mean flight time of animals, the electronically recorded time taken (in hundredths of a second) for an animal to cover a fixed distance (1.7 m) after leaving the weighing crush (Burrow *et al.* 1988) at various postweaning ages. Low flight times indicate poor temperaments and high flight times indicate desirable docile temperaments.

Table 6. Number of animals recorded for adaptive and temperament traits under study

	TICK	EPG	TEMP	COAT	FT
Number of records	4993	7229	8119	10841	15877
Number of animals	2346	2591	2540	2576	2555
Number of records per animal (range)	1-4	1-6	1-5	1-6	1-9
Average number of records per animal	2.13	2.80	3.20	4.21	6.21

In the COAT scoring system, each score was split into fractional scores to account for subclasses (for example, score 1 was again sub divided into 1-, 1, 1+ and 2 into 2-, 2, 2+ etc.,). For recording convenience, these fractional scores were converted as continuous numbers from 1 to 21 with 1-, 1, 1+ representing 1, 2, 3 and 2-, 2, 2+ representing 4, 5, 6 and so on. All analyses were conducted on converted scores (1 to 21) to increase the sensitivity of scores. Mean coat scores were calculated over all available coat scores for each animal, which were spread over the 10-month recording period across seasons. Initial analyses of data showed that coat scores followed the same pattern of sleek coats in summer and woolly coats in winter months across all breed groups.

3.3.2.2. Statistical analyses

Data on TICK, EPG, TEMP, COAT and FT were analysed using a univariate fixed effects model in ASREML (Gilmour *et al.* 2001). Model included the effects of genotype, contemporary group (consisting of year of birth, season of birth and age of dam) and sex, and previous lactation status of the dam. Treatment was also included as a fixed effect in the analysis of TEMP and FT data. Treatment was not significant for COAT and hence not included. Levels in the fixed effects were explained in the earlier section with growth traits. After testing the possible first order interactions for significance, all significant interaction effects were included in the analysis. Data pertaining to TICK and TEMP were subjected to $\log_{10}$ transformation and EPG were subjected to cube root transformation. Analyses were conducted both on transformed and non-transformed data. As the transformation did not affect the significance tests, only least squares means from non-transformed data are presented in this paper.

The method of crossbreeding parameter estimation is explained by Prayaga (2003*a*, 2003*b*, see appendix). Heterosis was estimated using least squares means for each trait as a deviation of the first cross (F_1) mean from the parental population mean and expressed as a percentage of the parental population mean. Heterosis estimates were only derived for those F_1 crosses where reciprocals existed.

3.3.2.3. Results and discussion

3.3.2.3.1. Genotype differences

Significant genotype differences were observed for various adaptive and temperament traits. Least squares means for the various adaptive and temperament traits are presented in Table 7. Over the years of study, mean tick counts ranged between 7.1 and 30.9 ticks per side and worm egg counts ranged between 216 to 770 eggs/gram of faeces, reflecting a low to moderate level of parasite infestation during the study. This is atypical of “normal” tropical climates in northern, coastal Australia. Despite these low to moderate tick and worm challenges, genotype differences in tick and worm egg counts were significant.

The overall mean TICK during the period of study was 18 ticks / animal, with (ZC)S having the highest mean TICK of 34.7 followed by BB (Belmont Adaptaur) with 29.1. It was interesting to note that despite being selected for tick resistance the Belmont Adaptaur line still had relatively low tick resistance. The lowest mean TICK was observed in ZxZ (9.5) followed by (BS)Z (9.9), and ZZ (10.3). Among purebreds, there was a clear distinction between BB and SS with high tick counts and ZxZx and ZZ with low tick counts. In crossbreds, as the Zebu proportion in the cross increased, TICK decreased. The observed increase in tick resistance with the increase in Zebu proportion in the cross was comparable to the results reported by Seifert (1971) and Lemos *et al.* (1985). Within F_1s, except in ZC, crosses with 50% Zebu proportion showed lower TICK with ZxZ and BZ having significantly ($P<0.05$) lower tick counts than BS. In F_1 backcrosses, lower tick counts were observed in (ZB)Z, (ZS)Z, and (ZZx)Z where the Zebu proportion was ≥ 75%. Low to moderate tick counts were observed in 3 breed crosses and 4-way crosses (F_1 x F_1) except in (ZC)S. The poorer tick resistance of Continental breeds was quite evident in this study, with high tick counts in ZC and (ZC)S, even though these genotypes had 25 to 50% Zebu content. This highlighted the vulnerability of Continental breeds to tick infestations.

Despite the significant genotype differences, even in the most resistant breeds and crosses at least 20% of animals can be categorised as lowly resistant or susceptible (Utech *et al.* 1978; Frisch 1999). To effectively breed for tick resistance in tropical environments, it is necessary to identify and cull the animals with low resistance and to select superior highly resistant males as parents of the next generation. Selection both within breeds and resulting crosses is essential in maintaining high levels of tick resistance, as the resistance gained through crossbreeding can be lost in later generations if inappropriate crosses are used or the inbreeding levels are increased.

The overall mean EPG was 458 eggs/g of faeces and varied between 274 ((ZB)Z) and 781 (SS) eggs/g. Among purebreds, ZZ had significantly ($P<0.05$) lower EPG followed by ZxZx with a significant difference between them. SS recorded significantly ($P<0.05$) higher EPG. Among F_1s, ZB had the lowest EPG and BS (100% *Bos taurus*) had the highest EPG. The effect of higher proportion of Zebu on reducing EPG was evident in F_1 backcrosses with (ZB)Z, (ZS)Z and (ZZx)Z (with ≥ 75% Zebu contribution) having lower mean EPG. All the 3 breed crosses with lower Zebu proportions had high mean EPG.

The overall mean TEMP was 39.47^0C and varied between 39.35^0C in (ZS)Z and 39.85^0C in BB. Among purebreds, British breeds (BB) were susceptible to high ambient temperatures, with significantly ($P<0.05$) higher rectal temperatures. The Zebu breed group had significantly ($P<0.05$) lower rectal temperatures (39.38^0C) demonstrating their resistance to heat stress. Among F_1s, ZxS, ZB, ZS, and ZZx (with ≥ 50% *Bos indicus*) had lower TEMP. In F_1 backcrosses, crosses with ≥ 75% of Zebu genetic contribution had lower TEMP. The lower TEMP in 3-breed crosses in the present study, even those containing only 25% Zebu showed that heat tolerance could be improved by proper crossing and exploitation of heterosis.

The overall mean COAT was 8.50 and varied between 7.20 (ZZ) and 12.05 (BB). This variation ranged from 3- to 4+ in the original scores, meaning coat was fairly short (generally smooth coated) in Zebus and fairly long (with the coat turning rough and with patches of hair being curved outwards) in the British breeds. SS and ZxZx had mostly similar and intermediate COAT. Coat type is a major determinant of temperature control and the similarities in the rankings of TEMP and COAT, at least in purebreds, shows the degree of interdependence between these traits. Among F_1s, ZS, ZxZ, and SZ had desirable lower COAT whereas SB, BS, and ZC had relatively higher COAT. Backcrosses with ≥ 75% Zebu contribution had sleek coats. Crosses with ≥ 75% British contribution (e.g. (ZB)B and (ZxB)B) had higher COAT indicating hairy and woolly coats.

Table 7. Least squares means of adaptive and temperament traits of various genotypes under study

Traits as defined in Table 5; N – number of records; Breed groups in genotypes as given in Table 1 with female breed given first in the crosses and crossbred dams and sires identified in parentheses, s- seconds, Differences between means >9.3, >168, 0.14°C, >0.38 and >0.15 (based on overall standard error of difference) are significantly different for TICK, EPG, TEMP, COAT and FT respectively

Genotype	N	TICK	N	EPG	N	TEMP (°C)	N	COAT	N	FT (s)
Overall	2346	18.0	2591	458	2540	39.47	2576	8.50	2555	1.37
Purebred										
BB	261	29.1	310	622	289	39.85	300	12.05	297	1.42
SS	209	27.9	226	781	224	39.53	227	8.78	223	1.41
ZxZx	56	12.3	56	498	55	39.50	56	8.73	55	1.44
ZZ	250	10.3	277	319	269	39.38	280	7.20	273	1.44
F_1										
BS	46	19.3	46	710	46	39.53	46	9.26	46	1.17
SB	22	18.0	23	554	22	39.64	23	9.67	23	1.49
BZ	93	10.3	94	458	95	39.56	94	8.68	94	1.26
ZB	98	13.2	115	291	112	39.42	113	8.34	113	1.41
SZ	139	13.0	139	492	135	39.48	136	7.78	135	1.30
ZS	157	16.0	178	431	177	39.42	177	7.65	176	1.39
ZZx	51	14.6	52	326	52	39.41	52	8.05	51	1.54
ZxZ	103	9.5	103	416	103	39.50	103	7.70	103	1.35
ZxS	52	17.1	55	570	53	39.40	56	8.46	56	1.40
ZC	79	26.3	91	320	90	39.50	91	9.26	91	1.43
F_1 backcross										
(ZB)B	56	22.5	56	402	56	39.59	56	9.35	56	1.32
(ZB)Z	108	13.1	121	274	120	39.40	121	7.70	120	1.35
(ZS)S	35	23.9	36	441	36	39.48	36	7.99	35	1.29
(ZS)Z	62	10.9	63	346	63	39.35	63	7.41	63	1.40
(ZZx)Z	19	12.5	20	352	18	39.45	20	7.67	20	1.44
(ZxB)B	42	23.7	50	523	50	39.63	50	10.11	50	1.57
(ZC)Z	39	14.9	43	399	43	39.42	43	8.15	43	1.37
3-breedcross										
(BS)Z	20	9.9	20	520	19	39.39	19	7.82	19	1.16
(ZB)S	97	21.3	114	520	113	39.43	114	8.38	114	1.31
(ZZx)S	35	12.9	35	466	35	39.47	35	8.02	35	1.45
(ZC)S	23	34.7	28	700	27	39.35	27	8.88	27	1.43
Z(BS)	37	20.0	39	511	39	39.47	39	7.86	38	1.22
S(ZC)	25	23.8	31	460	31	39.43	31	8.83	31	1.34
F_1 x F_1										
(ZB)(SZ)	30	16.4	45	302	44	39.35	44	8.20	44	1.29
(ZS)(SZ)	51	17.5	65	527	64	39.44	64	8.00	64	1.36
(ZS)(ZC)	28	21.7	33	293	32	39.39	33	8.43	33	1.37
(BS)(ZC)	23	21.5	27	373	27	39.54	27	9.01	27	1.24

The overall mean FT was 1.37s, varying from 1.16s in (BS)Z to 1.57s in (ZxB)B. Although significant genotype differences are observed for FT in the present study, there was no clear trend. All purebred genotypes had almost identical mean FT with no significant differences among them. In general, crossbreeding resulted in animals with slightly poorer temperaments without any significant improvement in FT relative to the purebreds. In a review, Burrow (1997) identified *Bos indicus* as more difficult to handle under extensive management conditions than either Sanga or other *Bos taurus* breeds. Results from the present study did not identify any such distinct differences.

3.3.2.3.2. Genetic effects

Direct and maternal additive and dominance effects provide evidence of the direction and magnitude of breed contributions for traits of interest. There are no other known reports in the literature on crossbreeding parameters for adaptive and temperament traits. However, these adaptive traits are of paramount importance in tropical environments. Hence, these parameters in combination with parameters for growth, add considerable value to the process of making crucial breeding decisions for tropical environments.

Crossbreeding parameters estimated for the adaptive and temperament traits are presented in Table 8. For all adaptive traits, direct breed effect of Zebu (aZ) was significantly negative (favourable) relative to the British breed mean (BB) suggesting better adaptation of Zebus. The direct breed effect of Sanga (aS) was significant and positive for EPG indicating an undesirable effect of worm egg counts in Sanga relative to British breeds. Hence, it was evident that though the tick resistance of Sanga and British breeds was similar, there were significant differences between the breeds in their resistance to worms. The similarity in tick resistance of British and Sanga breeds in the present study might be due to the selection for tick resistance in the Adaptaur line (British breed group) as explained earlier. However, a significantly ($P<0.01$) negative aS for TEMP and COAT indicated that Sanga derived breed groups (e.g. Belmont Red) were more heat resistant relative to the British breeds. The positive and significant aC (+21.7 ticks) for TICK emphasises that continental breeds are the least tick resistant breeds as also reported by Utech *et al.* (1978).

Table 8. Crossbreeding parameters for adaptive and temperament traits of various breed groups under study

a- breed additive, m – breed maternal, dD – direct dominance, mD – maternal dominance, II – indicine x indicine cross, TI – taurine x indicine cross, TT-taurine x taurine cross, S- Sanga, Zx- Zebu cross, Z – Zebu, C- Continental, negative effects are desirable for adaptive traits and positive effects are desirable for temperament

	TICK	EPG	TEMP	COAT	FT
Direct breed effect (direct additive)					
aS	2.4	252 **	-0.21 **	-2.37 **	-0.13 *
aZx	-14.7 **	-90	-0.28 **	-2.21 **	0.01
aZ	-21.6 **	-181 **	-0.32 **	-4.09 **	-0.16 **
aC	21.7 **	-76	0.03	1.25 **	0.01
Dam breed effect (maternal additive)					
mS	-1.7	-92	-0.05	-0.36 **	0.13 **
mZx	-0.9	-29	-0.05	-0.69 **	0.08
mZ	3.4	-130 **	-0.12 **	-0.48 **	0.18 **
mC	2.6	311 **	-0.07	0.17	0.14
Crossbreeding effect (direct dominance)					
dD_{II}	0.8	-36	0.01	-0.13	-0.03
dD_{TI}	-5.5 **	-80 **	-0.06 **	-0.60 **	-0.08 **
dD_{TT}	-7.7 **	-71	-0.13 **	-0.91 **	-0.10 *
Dam crossbreeding effect (maternal dominance)					
mD_{II}	-1.5	-54	0.02	0.13	0.08
mD_{TI}	1.1	-80 **	-0.07 **	-0.30 **	0.01
mD_{TT}	-0.8	-55	-0.09	-0.59 **	-0.09

*$P<0.05$, **$P<0.01$

Among dam breed effects, Zebu had desirable significantly negative (favourable) estimates for EPG, TEMP and COAT. The maternal influence of Zebu on worm resistance resulted in a significant decrease in faecal egg counts and could be due to the transfer of maternal antibodies that promote resistance from mother to calf either via colostrum or perhaps in-utero transfer. The importance of Zebu as a maternal breed in this tropical environment was also emphasised by the observation that except for TICK all other adaptive traits were favourably (negatively) affected by Zebu dam breed effect (mZ).

Based on the earlier results for growth traits (Prayaga 2003*a*) and from the present parameters on adaptive traits, Zebu or Zebu crossed with a taurine breed seems to be best suited as a maternal breed in a crossbreeding programme in the tropics. However, information on fertility traits would affect this observation, as Zebu breeds are known for relatively low fertility rates (Frisch *et al.* 1987).

Bos taurus x *Bos indicus* and *Bos taurus* x *Bos taurus* crosses benefited from heterosis as evidenced by significant negative crossbreeding effects (dD_{TI} and dD_{TT}) for all adaptive traits except for the dD_{TT} component in EPG. Crossbred (*Bos taurus* x *Bos indicus*) dams contributed significant and desirable negative maternal dominance effects (mD_{TI}) for EPG, TEMP and COAT traits. As the direct breed effects of Z for TICK and EPG were significantly negative and crossbreeding effect of (dD_{TI}) taurine x indicine cross was also significantly negative, the easiest way to increase tick and worm resistance from a British breed base in the breeding population was to increase the Zebu proportion through crossbreeding. Although resistance of crossbreds to specific stressors was perceived to be directly related to the proportion of resistant breeds in the cross (Lemos *et al.* 1985), implying an additive nature of resistance traits, the significant crossbreeding effects (dominance) in the present study highlighted the importance of crossing to exploit non-additive gene actions.

The similarity of additive and dominance effects of various breed groups for TEMP and COAT substantiates their interdependence to a certain extent. Among the genetic groups under study, British and Continental breeds were least resistant to heat as evident from the significantly negative (favourable) aS, aZx, and aZ relative to BB mean and the non-significant aC for TEMP observed in the present study. Significant and negative crossbreeding effects (dD_{TI} and dD_{TT}) for TEMP and COAT indicate these traits could be effectively improved by exploiting hybrid vigour through crossbreeding. *Bos indicus* x *Bos indicus* crosses did not benefit because of the lack of differences between their parental breeds in resistance to heat. Taurine crosses (TT) benefited because the parental breeds differ in their levels of adaptation to the tropical stressors. For example, the Belmont Adaptaur (Hereford – Shorthorn cross) that comprises the BB population in this study was selected for tick resistance for several generations (see Frisch *et al.* 2000). Hence it might have developed genetically dissimilar configuration to the other taurine breeds in terms of its tropical adaptability, thereby allowing significant expression of heterosis through dominance (dD_{TT}) for TICK, TEMP and COAT when crossed to the Sanga breeds, the other taurine group represented in this study.

3.3.2.3.3. Heterosis

Heterosis percentages ranged from -40 to 7% for TICK, -20 to -9% for EPG, -0.32 to 0.04% for TEMP, -11.6 to –1.1% for COAT and –6.6 to 0.3% for FT (Table 9). Negative heterosis was desirable for the adaptive traits and positive heterosis was desirable for temperament (FT).

Table 9. Heterosis percentages for selected genotypes for various adaptive and temperament traits

Traits as defined in Table 5; Genotype as shown in Tables 1 and 2; negative heterosis is desirable for adaptive traits and positive heterosis is desirable for FT.

	TICK	EPG	TEMP	COAT	FT
SB / BS	-35*	-10	-0.26	-9.1**	-6.0*
ZB / BZ	-40**	-20*	-0.32**	-11.6**	-6.6*
ZS / SZ	-24	-16*	-0.01	-3.4**	-5.6
ZZx / ZxZ	7	-9	0.04	-1.1	0.3

*P<0.05, **P<0.01

Direct heterosis estimates were significant and negative (desirable) for all the adaptive traits in Z and B crosses. In another *Bos taurus* x *Bos indicus* cross under study (i.e. Z and S crosses) heterosis was only significant for EPG and COAT. In crosses of S and B breed groups, significant and negative heterosis of –35% and –9.1% was estimated for TICK and COAT. In crosses involving Z and Zx, none of the heterosis estimates was significant, emphasising the degree of relatedness of these breed groups. For FT, average heterosis was significant and negative (unfavourable) for Z and B crosses and S and B crosses, suggesting that crossbreeding resulted in animals with poorer temperaments.

3.3.3. Effect of treatment to control ticks and worms on live weight gain

3.3.3.1. Statistical analyses

Live weight gain (kg) from 8 to 18 months (LWG) of age was estimated in various genotypes under study. A detail of recording of weights, ticks and worm egg counts was given in the previous sections. To study the effect of treatment on weight gain, LWG data were analysed using a univariate fixed effects model using ASREML (Gilmour *et al.* 2001). The model consisted effects of genotype, contemporary group, sex, treatment and previous lactation status of the dam. Age at final weighing was fitted as a covariate to adjust for the age differences. Significant first order interactions (genotype x treatment) were also included in the model. Least squares means of the treated and control animals within each genotype were derived from this analysis.

3.3.3.2. Results and discussion

Genotype means for LWG in treated and control animals are presented in Table 10 along with the response to treatment to control ticks and worms within each genotype. The overall LWG between 8 and 18 months was 129 kg in treated animals and 113 kg in control animals. Genotypes with highest and lowest LWG (ZC and BB respectively) ranked the same in both treated and control groups. Among all genotypes, SB (100% *Bos taurus*) benefited most (31 kg) by treatment and ZZx (predominantly *Bos indicus)* benefited the least (0 kg).

Among purebreds, treatment affected SS most, with treated animals gaining 26 kg more than controls. Zebus (ZZ) only benefited from treatment by 10 kg. As the *Bos indicus* proportion in the genotype increased, the benefit from treatment reduced, as evidenced by non-significant and low responses in ZZx, ZxZ and (ZZx)Z. However, significant responses in LWG from treatment among the majority of genotypes in the present study stressed the negative impact of parasite burdens on weight gain.

The response to treatment to control ticks and worms enables us to compare various genotypes for their potential to thrive in tick and worm infested areas. Based on these results, it can be concluded that treatment to control ticks and worms each 3 weeks does not improve the growth of Zebu animals to an economically viable extent. In British and Sanga breed crosses, treatment to control ticks and worms each 3 weeks significantly affected LWG, but even in those instances, careful consideration would need to be given to the economic viability of treating animals to the extent that occurred in this study.

Hence in a tropical environment where treatment may not be economically viable, various options to improve growth performance without investing on treatment to control parasites are: (i) Crossing indicine breeds when the parasite challenge is high as it exploits favourable direct and maternal additive effects of growth and adaptive traits and the dD_{II} effects for growth. (ii) Crossing taurine – indicine breeds where the parasite challenge is low to moderate and maintaining taurine purebreds is feasible, as it exploits desirable high dD_{TI} effects for growth and adaptive traits. Even in a high parasite challenge area this is a viable option if artificial breeding or tropically adapted taurine bulls can be used. (iii) Deriving and developing an optimal composite based on economic weights and crossbreeding parameters of growth and resistance traits (Prayaga *et al.* 2003).

Table 10. Effect of treatment on live weight gain of various genotypes under study

LWG – live weight gain from 8 to 18 months of age; response – treated LWG mean minus control LWG mean, genotypes as given in Tables 1 and 2, differences between genotypes >11.2 kg (based on overall standard error of difference) are significant

Genotype	N	LWG treated (kg)	LWG control (kg)	response
Overall	2475	129	113	16**
Purebred				
BB	278	112	88	24**
SS	218	131	105	26**
ZxZx	50	127	112	15**
ZZ	266	127	117	10**
F_1				
BS	45	118	103	15**
SB	20	123	92	31**
BZ	89	137	126	11**
ZB	108	135	122	13**
SZ	133	138	123	15**
ZS	167	140	123	17**
ZZx	50	124	124	0
ZxZ	100	129	120	9*
ZxS	52	127	110	17**
ZC	90	146	133	13**
F_1 backcross				
(ZB)B	56	121	102	19**
(ZB)Z	119	120	108	12**
(ZS)S	35	133	111	22**
(ZS)Z	63	130	115	15**
(ZZx)Z	17	132	117	15
(ZxB)B	49	112	91	21**
(ZC)Z	43	134	115	19**
3-breedcross				
(BS)Z	19	132	115	17
(ZB)S	111	124	108	16**
(ZZx)S	35	142	121	21**
(ZC)S	27	129	116	13
Z(BS)	39	132	118	14*
S(ZC)	29	135	113	22**
F_1 x F_1				
(ZB)(SZ)	44	133	108	25**
(ZS)(SZ)	64	119	107	12**
(ZS)(ZC)	32	132	113	19**
(BS)(ZC)	27	132	119	13

*P<0.05, **P<0.01

3.3.4. Buffalo fly scores

3.3.4.1. Data and statistical analysis

Buffalo fly lesions were scored on breeding cows from 1995 to 1998 at the time of weighing at mating break-up (out of mating) and at pregnancy diagnosis. These cows and heifers ranged in age from 2 to 12 years. Scoring was done by a single operator. Most of the literature reports on buffalo flies are based on buffalo fly numbers, as they are indicative of buffalo fly infestations. However, animals with high fly numbers are not always the animals that have big lesions or bleeding lesions, which cause production problems. Hence, buffalo fly lesion scores were scored on one side of the animal on a 1 to 10 scale as given below:

1 – no visible lesions
2 – one lesion less than or equal to 1 inch
3 – one lesion less than or equal to 3 inches
4 – multiple lesions e.g., 3 x 1 inch or 2 x 2 inches
5 – multiple lesions e.g., 4 – 6 lesions
6 – multiple lesions e.g., 7 – 10 lesions (7 to 10 square inches)
7 – multiple lesions – neck, belly, withers (at least 3 sites at 8 square inches)
8 – multiple lesions at least 3 sites on neck, belly, withers
9 – as per 8, only more extensive
10 – disaster

The 1856 records from 782 dams over the years 96 – 98 at out of mating (FLYOUT) and the 2401 records from 924 dams over the years 95 - 98 at pregnancy diagnosis (FLYPD) were included in the analysis. Genotype of cow, year of scoring, age of the dam and weight at the time of scoring were included in the model. Dam was included as a random effect as the scoring was done repeatedly every year. SB and ZxZx genotypes were not included in the analysis as there were very few animals recorded.

3.3.4.2. Results and discussion

The overall means for FLYOUT and FLYPD were 1.70 and 1.58 respectively indicating a very low level of buffalo fly lesions but with significant genotype differences (Table 11).

Table 11. Least squares means of buffalo fly scores at out of mating (FLYOUT) and at pregnancy diagnosis (FLYPD) for various genotypes of cows under study

Differences between means of >0.55 for FLYOUT and >0.46 for FLYPD are significant (based on overall standard error of difference)

	N	FLYOUT	N	FLYPD
Overall	782	1.70	924	1.58
		Purebred		
BB	138	2.84	174	2.56
SS	118	1.57	143	1.60
ZZ	147	1.83	204	1.56
		F_1		
BS	28	3.35	29	2.92
BZ	51	1.35	56	1.28
ZB	55	1.50	60	1.49
SZ	62	1.32	64	1.30
ZS	61	1.38	62	1.30
ZZx	17	1.16	18	1.05
ZxZ	50	1.25	53	1.15
ZxS	23	1.22	26	1.17
ZC	32	1.59	35	1.54

Both at out of mating and at pregnancy diagnosis similar trends occurred in buffalo fly scoring with similarities in the genotype means. British (BB) and British – Sanga cross (BS) showed relatively high incidence of buffalo fly lesions with higher scores than the other genotypes. Zebu and Zebu crosses with ≥ 75% of Zebu proportion showed less buffalo fly lesions with scores close to 1. These observations agree with the general perception of Zebu being resistant to external parasites while British breeds are more susceptible.

As the trait (buffalo fly lesion) was recorded as a score from 1 to 10 and as it was highly skewed, percentages of animals in each genotype in each of these categories of buffalo fly scores were tabulated (Table 12). For this comparison, buffalo fly scores were regrouped into 3 categories, as fewer numbers existed in many of these categories. These are:

1 – no visible lesions, similar to 1 in the previous scoring
2 – one lesion, equalling 2 and 3 of the previous scoring
3 – multiple lesions, equalling 4 and above of the previous scoring

Table 12. Percentage of animals in each category of buffalo fly scores at out of mating (FLYOUT) and at pregnancy diagnosis (FLYPD) categories in various genotypes

	Percentage of animals in FLYOUT categories				Percentage of animals in FLYPD categories			
	N	1	2	3	N	1	2	3
Purebred								
BB	108	19	61	20	111	25	57	18
SS	95	74	16	10	95	73	18	9
ZZ	120	67	20	13	136	76	15	9
F_1								
BS	30	23	37	40	30	40	23	37
BZ	49	82	12	6	49	82	14	4
ZB	51	79	11	10	51	80	12	8
SZ	60	85	9	6	61	87	8	5
ZS	58	86	9	5	56	89	6	5
ZZx	17	90	10		16	98	2	
ZxZ	50	87	8	5	49	91	6	3
ZxS	23	85	12	3	22	86	13	1
ZC	31	78	11	11	32	83	4	13

As shown in Table 12, Zebu crosses (ZZx and ZxZ) had ~ 90% of animals without any visible buffalo fly lesions. British breed group (BB) had 75 – 81% of animals with at least some buffalo fly lesions and only 19 – 25% with no visible signs emphasising the previous observation of susceptibility of the British breeds to buffalo flies. All the crossbred dams with at least 50% Zebu content had higher percentages of animals (75 – 98%) with no visible lesions. However, taurine crossbred dam (BS) had relatively lower percentages of animals (23 – 40%) with no visible lesions. Hence crossbreeding of taurine, indicine breeds is expected to increase buffalo fly resistance of the resulting genotype compared to taurine breeds.

3.3.5. Male fertility trait – Scrotal circumference (SC)

Scrotal circumference is a highly heritable trait with favourable correlations to semen characteristics and output (Coulter and Foote 1979), thereby making it an ideal trait for selection. Scrotal circumference is also reported to be a good indicator of age at puberty both in bulls and related heifers (Meyer *et al.* 1990 and references cited therein). Martin *et al.* (1992) reported favourable correlations between scrotal circumference and pregnancy rates in heifers.

3.3.5.1. Data and statistical analysis

Scrotal circumferences of the steer progeny of various genotypes produced in this study were measured at yearling age (YSC) and at final age of 18 months (FSC). YSC data were collected from 1268 animals and FSC data were collected from 1258 animals. A total of 30 genotypes ((ZZx)Z was dropped because of very few records) were compared based on breed pooling as described earlier in Tables 1 and 2. Data pertaining to YSC and FSC were analysed using a univariate fixed effects model (model 1) in ASREML (Gilmour *et al.* 2001), which included the effects of genotype, contemporary group (consisting of year of birth, season of birth and age of dam), treatment, and previous lactation status of the dam. Age of the animal at the time of measurement was also included as a covariate. Analyses were conducted with and without including weight at the time of measurement as a covariate. Year of birth ranged from 1992 to 1997 and months of birth were regrouped into 3 seasons (August – September, October – November and December – January). Age of dam at the time of calving was grouped into 3, 4, 5 and ≥ 6 years. Previous lactation status of the dam was categorised as wet (lactating) cow, dry (non-lactating) cow, cow with a dead calf and maiden heifer. When adjusted for weight, genotype x weight interaction was insignificant and hence dropped from the analyses.

3.3.5.2. Results and Discussion

The least squares means of various genotypes for YSC and FSC with and without weight adjustment are presented in Table 13. Even after adjusting for weight at respective ages of scrotal measurement, significant genotype differences existed in the present study indicating that the SC differences among various breed groups were independent of the weight differences to a certain extent.

Table 13. Least squares means of scrotal circumference at yearling age (YSC) and at final age of 18 months (FSC) for various genotypes under study

Differences between means of >16.1, >14.7, >15.6 and >15.0 mm (based on overall standard error of difference) are significant for YSC with and without weight adjustment and FSC with and without weight adjustments respectively

Genotype	N	YSC (mm) With wt. adjustment	YSC (mm) no wt.adjustment	N	FSC(mm) With wt. adjustment	FSC (mm) no wt.adjustment
Over all	1268	240	241	1258	286	286
Purebred						
BB	139	267	233	135	302	275
SS	114	247	245	113	293	290
ZxZx	25	234	221	25	274	267
ZZ	136	214	214	134	265	266
F_1						
BS	19	265	254	19	310	297
SB	12	261	246	12	301	289
BZ	40	249	245	39	295	294
ZB	49	236	240	49	273	275
SZ	62	244	252	63	295	301
ZS	99	220	225	100	267	273
ZZx	33	217	215	33	266	263
ZxZ	49	232	233	49	279	282
ZxS	28	241	244	28	290	294
ZC	47	218	233	47	270	284
F_1 backcross						
(ZB)B	34	242	242	34	288	285
(ZB)Z	66	238	237	65	288	289
(ZS)S	18	237	243	18	279	284
(ZS)Z	30	240	245	28	287	293
(ZxB)B	22	269	261	21	303	288
(ZC)Z	21	223	236	21	281	289
3-breedcross						
(BS)Z	10	262	272	10	300	318
(ZB)S	56	238	244	55	281	285
(ZZx)S	18	227	241	18	274	283
(ZC)S	15	227	247	15	286	293
Z(BS)	19	246	247	19	287	291
S(ZC)	17	248	255	18	287	290
F_1 x F_1						
(ZB)(SZ)	26	243	241	26	284	284
(ZS)(SZ)	30	228	226	30	273	270
(ZS)(ZC)	21	249	250	21	291	296
(BS)(ZC)	13	253	253	13	299	302

When adjusted for weight, YSC and FSC of (ZxB)B, BB and BS (with ≥ 87.5% taurine proportion) were high and that of ZZ and ZZx remained unchanged and low. With no weight adjustment, a sharp decline in the scrotal circumference of BB was noticed in both YSC and FSC emphasising the importance of adjusting for weight while analysing scrotal circumference and also showing the high scrotal circumference of British breeds relative to their body weights. The Zebus (ZZ) were unaffected by the adjustment for weight with virtually no change in their scrotal circumferences. ZC also showed a decline in scrotal circumference when adjusted for weight as expected because of their heavier body weights.

Percent heterosis estimates for YSC and FSC with and without adjustment in various F_1 crosses are presented in Table 14. Heterosis percentages were low and insignificant for scrotal circumference at yearling age and final age when the adjusted for weight indicating that the heterosis in SC was a consequence of heterosis gained through increased weight. Gregory *et al.* (1991*b*) also reported that much of the heterosis for SC was removed when adjusted for weight. A significant negative effect of Zebu was seen in the least squares means of YSC and FSC in reciprocal crosses of BZ / ZB, SZ / ZS and ZZx / ZxZ, with SC being lower whenever Zebu was used as a dam.

Hence, from the present results it can be interpreted that the semen characteristics and seminal volume of British bulls would be higher than that of Zebu and its crosses based on the reported correlations between scrotal circumference and the semen volume and semen characteristics. Sanga derived crosses are also rated higher than the Zebu in male fertility traits. These conclusions are based on the high correlation between SC and other male fertility traits from literature reports. It can also be expected that British breeds excel in female fertility traits relative to Zebu because of the favourable correlations between SC and female fertility traits.

Table 14. Percentage heterosis estimates of scrotal circumference at yearling age (YSC) and at final age of 18 months (FSC) in various F_1 crosses
Genotype as shown in Tables 1 and 2

Genotype	YSC with weight adjustment	YSC no weight adjustment	FSC with weight adjustment	FSC no weight adjustment
SB / BS	2.3	4.6	2.7	3.7
ZB / BZ	0.8	8.5**	0.2	5.2**
ZS / SZ	0.7	3.9*	0.7	3.2*
ZZx / ZxZ	0.2	3.0	1.1	2.3

*P<0.05, **P<0.01

3.3.6. Female fertility traits

3.3.6.1. Calving success (CS)

3.3.6.1.1. Data and statistical analysis

Calving success was recorded as a binomial trait, 0 - no calving and neonatal mortalities and 1 - successful calving with live calf at birth. Calving success data from matings (both natural and AI / backup bull) of years 92 to 98 were analysed. Data from 1991 mating was excluded from analyses because of flooding and subsequent regrouping of cows in the mating families. From preliminary analyses, there were significant differences in the female fertility of Borans and Brahmans. Because of this and also as the trait was recorded on the parental generation (cows) rather than progeny, breed pooling was not done in the present analyses of female fertility traits. The breeds (not pooled breed groups) involved in the study of the female fertility traits are given in Table 1.

Female fertility traits were analysed as traits of the dam. The model for analysis included dam breed, bull breed, contemporary group (including year of mating and age of the dam) with into mating weight of the cow being included as a covariate. As there were breed differences between wet (lactating) and dry (non-lactating) cows in calving success, analyses were conducted separately for wet and dry cows. For wet (lactating) cows, previous day of calving was included as a covariate to adjust for the differences in early and late calving. PLS (previous lactation status of the cow) for wet cows was divided into 4 classes depending on the breed and sex of the previous calf i.e., purebred male, purebred female, crossbred male and crossbred female calves. However, it had no significant effect in the present study. For dry cows, PLS (heifer or dry cow) was included in the model as a fixed effect. PLS of dry cows comprised of dry – non pregnant, dry – abort, dry – neonatal mortality, dry – calf dead between one week to out of mating categories. Dam was included as a random effect to account for the repeated observations on the same dam.

For wet cows, 2896 records from 1331 dams at the rate of 2.18 records per dam and for dry cows, 1411 records from 1199 dams at the rate of 1.18 records per dam were included in the analyses. In the case of dry cows, records were only repeated in a limited number of cows as this group predominantly contained maiden heifers. CS was expressed as a proportion between 0 and 1 and can be converted to a percentage by multiplying with 100. All analyses were conducted using binomial trait models with ASREML (Gilmour *et al.* 2001). Data from mating families with 10 - 50% calving successes (6 bulls) were deleted from the analyses as these values were assumed to have arisen from bull failures.

3.3.6.1.2. Results and Discussion

Genotype means of calving success proportions for wet (lactating) and dry (non-lactating) cows are presented in the tables 15 and 16 respectively. Overall, maiden heifers and dry cows (Table 16) had higher calving success than wet cows (Table 15). In wet cows, Belmont Adaptaur (HS) had higher calving success (0.71) of all purebreds. BX purebreds had very low calving success (0.58) in wet cows. Seebeck (1973) found that wet Zebu cross cattle had relatively low fertility while the wet British cattle had relatively high fertility. Though lower fertility in wet Brahman cows compared to wet HS cows was observed in the present study, Brahmans did not show any striking low fertility levels. Hence, the general perception that Brahmans are less fertile than the other breeds is not substantiated in this study. Frisch (unpublished data) opined that the high performance of straightbred Brahmans might be due to the presence of a highly fertile family of cows. O'Neill *et al.* (2000) also stated that the Brahman herd at Belmont had phenotypically high fertility.

Table 15. Least squares mean calving success of various cow genotypes – wet (lactating) cows
Number of animals given in parentheses; standard errors ranged between 0.03 and 0.11

	Sire breed of the dam							
Dam breed of the dam	HS	AX	BX	Bh	Ch	Bo	Tu	Dam breed mean[a]
HS	0.71 (208)			0.66 (33)		0.96 (16)	0.84 (26)	0.82
AX		0.60 (160)		0.87 (32)		0.74 (27)	0.75 (31)	0.79
BX			0.58 (116)	0.75 (24)		0.78 (27)	0.66 (22)	0.73
Bh	0.67 (92)	0.70 (42)	0.67 (15)	0.63 (342)	0.52 (51)	0.78 (16)	0.84 (15)	0.70
Sire breed mean[a]				0.76		0.82	0.77	

[a] Crossbred means within common sire or dam breed of the dam

Crossbreds in general had better calving success than purebreds and the crossbred advantage was more evident in wet cows than in dry cows. Brahman purebred dry cows (which consisted predominantly of heifers) had higher CS (0.90) than the wet cows (0.63). Frisch *et al.* (1987) also reported that lactating Brahmans produced markedly lower calf crops than their non-lactating contemporaries and the HS cows were as fertile as their non-lactating contemporaries. In the present study, the CS of HS wet cows (0.71) was comparable to that of dry cows and maiden heifers (0.80). The Brahman crosses with AX, BX and Ch also had lower CS for wet cows compared to the contemporary dry cows. This is probably due to the Zebu cross having greater incidence of lactational (post partum) anoestrus (Baker, 1969).

Table 16. Least squares mean calving success of various genotypes – dry (non-lactating) cows and maiden heifers

Number of animals is given in parentheses; standard errors ranged between 0.03 and 0.14

	Sire breed of the dam							
Dam breed of the dam	HS	AX	BX	Bh	Ch	Bo	Tu	Dam breed mean[a]
HS	0.80 (194)			0.89 (36)		0.88 (18)	0.95 (29)	0.91
AX		0.89 (127)		0.71 (36)		1.00 (28)	0.94 (34)	0.88
BX			0.92 (85)	0.86 (26)		1.00 (27)	0.74 (25)	0.87
Bh	0.93 (108)	0.90 (46)	0.83 (19)	0.90 (234)	0.95 (54)	0.88 (16)	0.93 (15)	0.90
Sire breed mean[a]				0.82		0.94	0.89	

[a] Crossbred means within common sire or dam breed of the dam

The crossbred cow CS means within common sire or dam breed of origin were also presented in tables 15 and 16. For example, 0.82 HS dam breed mean refer to the crossbred F_1 cows with common HS origin (dam breed of the dam) calving success mean. Crossbred means of HS, AX, BX and Bh dam breeds of the dams were 0.82, 0.79, 0.73 and 0.70 (Table 15) respectively in wet cows, which were significantly higher than their respective purebred means of 0.71, 0.60, 0.58 and 0.63 respectively. In dry cows, CS crossbred means of HS dam breed of the dam (0.91) only was significantly higher than purebred mean (0.80) (Table 16). Hence the crossbred advantage of cows in fertility traits is more pronounced in wet cows than the dry cows. Bo sired crossbred cows had higher calving success in wet (0.82) and dry (0.94) cows than that of Bh sired crossbred cows showing the advantage of Boran over Brahmans in fertility traits.

3.3.6.2. Days to Calving (DTC)

3.3.6.2.1. Data and statistical analysis

Days to calving (DTC) was calculated as the number of days from when the bull went into the mating paddock until the cow calved. It was estimated for all the cows joined by natural mating. DTC for the cows that did not calve was calculated as the highest DTC in that contemporary group (year of mating) + 21 days (Johnston and Bunter, 1996). The model included dam breed, bull breed, contemporary group (year of mating and age of the dam) and previous lactation status (PLS) as fixed effects, and previous day of calving in wet (lactating) cows and into mating weight as covariates. Dam was included as a random variable. The 2285 records on DTC from 1175 dams were included in the analysis.

3.3.6.2.2. Results and Discussion

Among purebreds, lowest most (favourable) DTC was observed in HS and Brahmans also recorded relatively low DTC (Table 17). The highest (unfavourable) DTC was in BX. Bo sired crossbred cows had lower DTC especially in their crosses with HS and Bh. Brahman crossbred dams generally recorded lower DTC than the purebred Brahmans except in Bh x Ch. Bh x AX and Bh x Bo crossbred dams had the lowest (324) DTC among all the crosses under study. Hence, a clear advantage of crossbred dams over purebred dams was noticed in DTC. The crossbred dam advantage was evident in common dam breeds of AX, BX and Bh with crossbreds (335, 332 and 329 respectively) having lower mean DTC than the purebreds (340, 349 and 336 respectively).

Table 17. Least squares mean days to calving (DTC) in various genotypes from natural matings
Number of animals in each genotype is given in parentheses; standard errors ranged between 4 and 8

	Sire breed of the dam							
Dam breed of the dam	HS	AX	BX	Bh	Ch	Bo	Tu	Dam breed mean[a]
HS	330 (196)			335 (31)		325 (14)	331 (26)	330
AX		340 (144)		331 (26)		335 (26)	339 (25)	335
BX			349 (110)	331 (24)		330 (19)	336 (22)	332
Bh	330 (90)	324 (32)	327 (16)	336 (270)	339 (46)	324 (11)	331 (13)	329
			Sire breed mean[a]	332		329	334	

[a] Crossbred means within common sire or dam breed of the dam

3.3.6.3. Heterosis in female fertility traits

The percent heterosis estimates on female fertility traits of calving success and days to calving are presented in Table 18. In general, heterosis estimates were low and insignificant except in the wet cows of Brahman and Belmont Red cross for CS. Percent heterosis was significant but of low magnitude in DTC in Bh / AX and Bh / BX crosses.

Table 18. Percentage heterosis estimates for the female fertility traits of calving success (CS) and days to calving (DTC)
For DTC, negative heterosis is favourable

	Calving success (wet cows)	Calving success (dry cows and maiden heifers)	Days to calving
Bh / HS	-0.75	7.1	-0.2
Bh / AX	27.6**	-10.1	-3.1*
Bh / BX	17.4	-7.1	-3.9*

*P<0.05, **P<0.01

3.3.7. Calf survival traits as a measure of calf mortality

Calf survival can be regarded as a trait of the dam before weaning and also as a trait of the calf. In the present study, as the breed differences are of interest, proportion of calves surviving until one week after birth and weaning were estimated and compared among various genotypes of the dams and also among various calf genotypes based on breed pooling. Preweaning calf mortality in the present study was recorded from 1 to 11 as described with their respective percentages below.

Calf mortality code	Description	number	Mortality percentage of the total mortalities
Calf alive at birth		2765	
1	Calf is normal / alive at birth	2765	
Calf dead		321	
2	Calf aborted	162	50.5
3	Calf died from dystocia	28	8.7
4	Calf died due to the mothering ability such as bottle tits and abandoning of the calf	7	2.2
5	Unknown (neonatal mortality - one week)	44	13.8
6	Unknown (one week – into mating with the dam)	29	9.0
7	Unknown (into mating with the dam – weaning)	26	8.1
8	Calf died because cow died or very sick	9	2.8
9	Misadventure – calf gets run over, drown in river	2	0.6
10	Calf is premature	1	0.3
11	Calf killed by dogs	13	4.0

Preweaning mortalities constituted 10.4% (321 of 3086) of the total births. Abortion was the major cause of calf mortality and accounted for 50% of the calf preweaning mortalities and 5% of the total calvings. Other causes like dystocia, due to unknown reasons between birth to one week followed next. For the purpose of analyses, calf survival was coded as a binomial trait as: 0 – calf is dead and 1 – calf is alive at a given stage of life. Calf mortalities due to attack by dogs (code 11) and calf gets run over (code 9) were not included as mortalities as it was neither the fault of the calf nor the cow. Data pertaining to calf deaths due to twinning were not included in the analyses.

3.3.7.1. Data and statistical analyses

It was observed that 80% of the calf mortalities before weaning occur within one week of birth. Hence, the aim was to compare breed differences for calf survival up to one week (WKS) and up to weaning (PWS). The 3086 calf survival records from 1413 dams of various genotypes were included in the analysis when survival was treated as a trait of the dam. Analyses included dam breed (breed codes as given in Table 1), bull breed, contemporary group (year of birth and age of the dam), previous lactation status of the dam (PLS) and sex as fixed effects and birth weight as a covariate with a spline component as a random effect for birth weight to account for its non-linear relation with survival. Dam was included as a random effect in the model because of the repeated records on the dam. Missing values existed in sex, bull breed and birth weight, as the calves that aborted and some that died immediately after birth were not recorded for their sex and birth weight. Bull breed in some of these calves could not be determined as they could have been by either AI or back up bull matings. These records were also included in the analyses by treating the missing information in the design variables as missing values thereby treating them as a separate effect.

The 2815 calf survival records where calf breed was identified were included in the analysis when survival was treated as a trait of the calf. The model included the effects of calf breed, contemporary group, PLS, and sex. Birth weight was fitted as a covariate. Postweaning calf survival to 18 months of age (POSTWS) was also analysed as a trait of the calf.

3.3.7.2. Results and discussion

Birth weight had a non-linear relationship with survival proportions and the calves with higher or lower birth weights i.e., 1.5 – 2 phenotypic standard deviations on either side of mean had lower survival proportions compared to calves with birth weight around mean. Gregory *et al.* (1991*a*) also reported that calf survival at weaning was lowest for the smallest ($<\mu - 1.5\ \sigma$) and largest ($>\mu + 1.5\ \sigma$) birth weight classes and did not differ among intermediate birth weight classes in temperate environments.

Breed differences in calf survival were noticed even after adjusting for calf sex and birth weight differences emphasising that differences in calf survival between dam breeds (Tables 19 and 20) and calf genotypes (Table 21) are independent of calf sex and birth weights. Note the differences in number of cow (Tables 19 and 20) and calf records (Table 21) included in the analyses between genotypes stressing the need for caution while drawing conclusions.

3.3.7.2.1. Calf survival as a trait of the dam

Calf survival up to a week after birth (WKS) and preweaning calf survival (PWS), given as proportion between 0 and 1, in various cow genotypes are presented in Tables 19 and 20 respectively. These can be converted to percentages by multiplying with 100.

Table 19. Least squares mean survival of the calf to one week after birth (WKS) in various cow genotypes

Number of animals is given in parentheses; standard errors ranged between 0.01 and 0.07

	Sire breed of the dam							
Dam breed of the dam	HS	AX	BX	Bh	Ch	Bo	Tu	Dam breed mean[a]
HS	0.89 (218)			0.97 (35)		0.97 (16)	0.96 (29)	0.97
AX		0.96 (167)		0.99 (34)		1.00 (28)	0.98 (32)	0.99
BX			0.96 (151)	0.99 (24)		0.99 (27)	0.94 (24)	0.97
Bh	0.97 (84)	0.98 (24)	0.99 (17)	0.96 (382)	0.97 (49)	0.97 (16)	1.00 (15)	0.98
Sire breed mean[a]				0.98		0.98	0.97	

[a] Crossbred means with in common sire or dam breed of the dam

Table 20. Least squares mean survival of the calf to weaning (PWS) in various cow genotypes

Number of cows is given in parentheses; standard errors ranged between 0.01 and 0.07

	Sire breed of the dam							
Dam breed of the dam	HS	AX	BX	Bh	Ch	Bo	Tu	Dam breed mean[a]
HS	0.84 (218)			0.94 (35)		0.91 (16)	0.93 (29)	0.93
AX		0.92 (167)		0.98 (34)		0.98 (28)	0.97 (32)	0.98
BX			0.92 (151)	0.96 (24)		0.98 (27)	0.90 (24)	0.95
Bh	0.96 (84)	0.97 (24)	0.98 (17)	0.93 (382)	0.95 (49)	0.96 (16)	1.00 (15)	0.97
Sire breed mean[a]				0.96		0.96	0.95	

[a] Crossbred means with in common sire or dam breed of the dam

Purebred dams of HS (Belmont Adaptaur) calves had lower WKS and PWS than other purebred dams such as AX, BX and Bh. Brahman (Bh) purebred dams had lower PWS (Table 20) than crossbred Bh dams, though not statistically significant, emphasising the advantage of crossbred dams. Though HS crossbred dams with Bo and Tu had improved preweaning survival rates relative to HS purebreds, they still had lower survival rates than other crossbred dams. AX crossbred dams with Brahman, Boran and

Tuli had higher WKS and PWS than purebred AX dams.

The preweaning calf survival rates show a clear advantage to crossbred dams relative to purebred dams (particularly HS dams). The purebred HS survival at weaning (0.84) was significantly lower than the survival rate in HS crossbred dams (0.93). To explore further the poorer performance of British dams (HS) compared to other purebreds and crossbreds, the survival proportions were also analysed as traits of the calf.

3.3.7.2.2. Calf survival as a trait of the calf

Differences due to calf genotype in calf survivals up to a week after birth (WKS), to weaning (PWS) and postweaning up to 18 months of age (POSTWS) are presented in the Table 21.

Table 21. Least squares mean survival of calf up to one week after birth (WKS), to weaning (PWS) and to 18 months of age (POSTWS) for various calf genotypes under study

Standard errors ranged between 0.02 and 0.13; N – number of records; Genotypes as given in Tables 1 and 2

Genotype	N	Calf survival to one week after birth (WKS)	Preweaning calf survival (PWS)	Post weaning calf survival (POSTWS)
		Purebred		
BB	351	0.92	0.89	0.85
SS	244	0.96	0.92	0.91
ZxZx	73	0.93	0.80	0.80
ZZ	317	0.93	0.90	0.90
		F_1		
BS	53	0.98	0.98	0.93
SB	27	1.00	1.00	0.95
BZ	111	0.86	0.84	0.84
ZB	121	0.96	0.96	0.94
SZ	156	0.95	0.93	0.92
ZS	201	0.97	0.95	0.94
ZZx	61	0.92	0.91	0.89
ZxZ	110	0.96	0.96	0.96
ZxS	66	0.95	0.92	0.91
ZC	98	0.97	0.96	0.92
		F_1 backcross		
(ZB)B	59	0.98	0.98	0.98
(ZB)Z	127	0.97	0.96	0.96
(ZS)S	37	0.95	0.95	0.94
(ZS)Z	67	0.98	0.95	0.95
(ZZx)Z	24	0.94	0.87	0.75
(ZC)Z	46	0.98	0.97	0.97
		3-breedcross		
(BS)Z	22	0.88	0.87	0.87
(ZB)S	121	0.99	0.98	0.97
(ZZx)S	36	1.00	1.00	1.00
(ZC)S	30	1.00	1.00	0.96
Z(BS)	43	0.93	0.89	0.89
S(ZC)	31	1.00	1.00	1.00
		F_1 x F_1		
(ZB)(SZ)	51	0.92	0.87	0.87
(ZS)(SZ)	68	0.93	0.93	0.93
(ZS)(ZC)	34	1.00	1.00	0.97
(BS)(ZC)	30	0.90	0.90	0.90

The calf genotypes are based on breed pooling as shown in Tables 1 and 2. British purebreds had high WKS, but lower POSTWS indicating higher mortalities in British purebreds. Preweaning survival of ZxZx (0.80) was lowest among purebred calf genotypes while Sanga (SS) had relatively high survivals at all ages.

WKS of BZ calves was significantly lower than ZB and even purebred calves of the parental breeds. Dystocia was observed mostly in British dams (14 out of total reports of 22 cases), which was the reason for the lower WKS in the BZ calf genotype i.e. British (HS) dams sired by Zebu bulls. This also explained the lower survival rates in HS dams in WKS and PWS (Tables 19 and 20) when survival was analysed as a trait of the dam. Frisch (unpublished data) also reported that most of the mortalities of Zebu sired calves were associated with dystocia in maiden heifers or losses of drought affected maidens weakened further by calving. Gregory *et al.* (1979) found that more calving assistance was required for Brahman sired, first cross calves out of Hereford and Angus cows than for other sire breeds. This is comparable to the incidence of more dystocia in BZ calves with British dams and Zebu sires and hence low survival rates in the present study. In this study, Zebu crossbred (ZZx)Z, with predominantly Zebu content, had relatively lower survival rates both at weaning (87%) and 18 months (75%). The low number of records in this genotype suggested that a scaling effect might partially be responsible for these values.

The majority of crossbred calves had higher survival rates than any of the purebred genotypes at weaning and also at 18 months of age. Among F_1 genotypes, except for BZ, all genotypes had high survival rates. Williams *et al.* (1990) reported that crossbred calves produced in various rotational mating systems generally had higher survival rates than straightbred calves. In the crossbreeding parameters estimated for calf survival by Williams *et al.* (1991), direct and maternal additive effects of Angus, Brahman, Charolais, and Hereford in a subtropical environment were relatively small and not different from zero. The only significant heterotic genetic effect for calf survival was that of maternal heterosis of Brahman x Hereford crossbred dams.

3.3.7.2.3. Heterosis in calf survival traits

The percent heterosis estimates of the calf survival traits are presented in Table 22. Although the majority of the estimates were positive, they all were mostly insignificant except in the case of BS / SB and ZZx / ZxZ when the trait was estimated as a trait of the calf. Williams *et al.* (1990) also reported low heterosis percentages for calf survival. Gregory *et al.* (1991*a*) reported that heterosis effects on survival up to weaning generally were positive, but not significant.

Table 22. Percentage heterosis estimates for survival traits such as survival of the calf to one week after birth (WKS), to weaning (PWS) and to 18 months (POSTWS)

	WKS	PWS	POSTWS
Calf survival as trait of the dam			
Bh / HS	4.9	7.3	
Bh / AX	2.6	5.4	
Bh / BX	3.1	4.9	
Calf survival as trait of the calf			
BS / SB	5.3	9.4*	6.8
BZ / ZB	-1.6	0.6	1.7
SZ / ZS	1.6	3.3	2.8
ZZx / ZxZ	1.1	10.0**	8.8*

3.3.8. Carcass and meat quality traits

Gazzola *et al.* (1998)

As part of this study, the possibility of the existence of Brahman sires whose progeny have high marbling scores and high intramuscular fat content was investigated. A Brahman sire (Select sire) whose progeny had both high marbling scores and high intramuscular fat, independent of the dam breed, was identified in both grain and pasture finished systems. This Select sire's progeny were equal to or better than progeny from Tuli sires, which have typical *Bos taurus* marbling characteristics producing high marbling scores. The intramuscular fat content of the progeny from the Select sire was greater than that of progeny from other Brahman sires and higher than progeny from Tuli sires. This increased marbling and intramuscular fat content were not associated with increased subcutaneous fat deposits, decreased muscle deposition, lower growth rate or smaller mature size since there were no differences in age, hot standard carcass weight, rump fat depth and rib eye muscle area between Select sire's progeny and those of the Brahman sires. Hence there is a possibility of not only introducing the trait into other Brahmans but also for farming tropically adapted, high marbling crossbreds, or composites based on the Select sire and other high marbling breeds such as Angus, Shorthorn, Tuli and Belmont Red.

Gazzola *et al.* (1999)

Breed groups ranging from 100% *Bos indicus* to 100% *Bos taurus* content were derived from Zebu (Brahman), African zebu (Boran), British breeds (Hereford-Shorthorn), Continental breeds (Charolais and Simmental) and Sanga (Tuli and Belmont Red) involved in this crossbreeding study. Progeny were raised at pasture in a tropical environment and finished either on pasture or in a feedlot were compared for meat quality characteristics to determine influence of environment in which the animals were finished.

The major observation of this study was that the tenderness of grilling and roasting cuts of meat from the predominantly Brahman-based beef herd of northern Australia can be improved through crossbreeding with any of the taurine breeds studied. There was no evidence of heterosis in any eating quality characteristics, so the F_1 crosses will always produce meat with eating quality attributes between those of the two parental breeds.

For striploins (*longissimus*) from feedlot finished steers, cooking loss was greatest for Zebu steaks, least for British steaks and intermediate for other breeds. For striploins from pasture finished steers and eye rounds (*semitendinosus*) from both pasture finished and feedlot finished steers, there were no breed differences in cooking loss. For both feedlot finished and pasture finished steers, striploin steaks from British steers were most tender, and Sanga (S) and Zebu x Continental cross (ZC) steaks were more tender than Zebu steaks.

3.4. Applications

The major achievement of this crossbreeding study is the quantification of the differential performance of various crosses in this tropical environment of low to moderate parasite challenge. Two options have been outlined here to fully utilise this knowledge of crossbreeding parameters in improving breeding programmes.

3.4.1. Decision support software

One of the applications of these crossbreeding parameters estimated in the present study is through development of prediction models to estimate the performance of untested genotypes. Though it is easy to visualise the concept of utilising these parameters for the prediction models, in reality it can be a quite complex task as the production systems and the economic importance of various traits in various environments differ. For example, while tick resistance may be a major trait of economic importance in the northern parts of Australia, it is not important in tick free areas of southern Queensland. Worm resistance may be a trait of importance in coastal regions but not in inland properties. Hence understanding the importance of resistance traits and quantifying their net economic values at least in certain stratified classes such as low, medium and high parasite challenge is of great importance in the development of decision supporting tools or prediction models for tropical beef cattle breeding. The parameters developed in the present study along with certain parameters available from other crossbreeding experiments can be useful in the development and refinement of DSS like HOTCROSS.

3.4.2. Optimal breed proportions in tropical beef composites

Another application of the knowledge gained through the present study is to optimise breed proportions in tropical beef composites for various environments. Systematic crossbreeding or the production of composites is the best way of exploiting both additive and non-additive gene action in beef cattle. Once established, composites can be maintained as a straightbred population and hence have an advantage over systematic crossbreeding. Newman *et al.* (1998) described the optimisation of breed proportions in tropical environments based on growth traits alone. Hayes *et al.* (2000) stated that optimal composites based on growth traits alone might not represent the true economic merit of the composite. Resistance to ticks and worms plays an important role in determining growth and survivability in the tropics. Hence, this information should be included in optimisation models. As an example of the usage of these growth and resistance trait parameters, optimal breed proportions in tropical beef composites at various assumed levels of parasite challenge are derived and presented below. The methodology of optimisation procedure, crossbreeding parameters and economic weights used in the procedure are given by Prayaga *et al.* (2003, see appendix).

When only growth traits were considered for optimisation, the control group (based on animals not treated to control ticks and worms) optimal breed proportions in the composite were 36% and 64% for Z (Zebu) and C (Continental) respectively (Table 23). This was comparable to the two-breed optimal composite of Brahman (32%) and Charolais (68%) suggested by Newman *et al.* (1998). Based on treated group genetic parameters, an increase in the proportion of C and a decrease in Z was evident with optimal breed proportions of 24.4% and 75.6% of Z and C respectively.

At very low TICK (tick counts), EPG (worm egg counts) or both the optimal breed proportions of Z in the composite ranged between 30.0 – 37.7% and the C proportions ranged between 62.3 – 70.0% indicating only a slight deviation from the optimal proportions derived from growth traits alone. At medium tick levels, the C breed proportion reduced to 49.2% and Z proportion increased to 50.8%. Hence, at medium tick levels, optimal breed proportions derived by including tick count information reduces the non adapted breed proportion to <=50% even without constraining its proportion as described by Hayes *et al.* (2000). At high tick levels alone or at medium or high tick and worm infestations, S (Sanga) entered into optimal breed proportions. As the S breed group had high faecal egg counts (Prayaga 2003*b*), its proportion in the optimal composite was high only when growth traits + TICK were considered. But its proportions reduced when both TICK and EPG were considered along with growth traits. At high tick and worm levels, the Zebu breed (91.9%) was the predominant component of the optimal composite together with Sanga (8.1%). The Continental breed group was no longer represented in the optimal composite because the negative influence of high tick and worm egg counts outweighed the growth benefits.

Table 23. Breed proportions in optimal composites under various assumed levels of parasite challenge

	Breed Proportions		
Traits	Sanga	Zebu	Continental
I. Growth traits			
a. WWT+FWT (treated)	-	24.4	75.6
b. WWT+FWT (control)	-	36.0	64.0
II. Growth traits + TICK			
Low	-	30.0	70.0
Medium	-	50.8	49.2
High	18.7	66.7	14.6
III. Growth traits + EPG			
Low	-	32.6	67.4
Medium	-	56.0	44.0
High	-	73.6	26.4
IV. Growth traits +TICK +EPG			
Low	-	37.7	62.3
Medium	3.9	72.0	24.1
High	8.1	91.9	-

Further studies to derive economic weights for tick and worm egg counts at various levels of parasite challenge could provide more accuracy to these evaluations. The present study assumed the availability of all possible breed groups while deriving the optimal composites, but it can also be utilised in more practical situations where only particular breeds are available to develop tropically adapted composites.

3.5. Conclusions and recommendations

As a ready-reckoner for the differences in the performance of various breed group combinations in various traits under study, the following table (Table 24) presents the relative rankings on a scale of one to four stars, where one star indicated poor performance for the trait of interest and four stars indicated good performance. These are only indicative relative performances derived based on least squares means and crossbreeding parameters, to be used to place the performance of a particular cross relative to others in various economic traits. These rankings apply only to a tropical environment with a low to moderate parasite challenge. The rankings for all traits are likely to change under conditions of either no or very high parasite challenge.

Table 24. Differential indicative performance ranking of various combinations of dam and sire breed groups for various traits recorded in a tropical environment with low to moderate parasite challenge

B- Tropically adapted British (Hereford-Shorthorn), S- Sanga derived, Z- Zebu, C-Continental, * denotes poor performance for the trait of interest and increments up to **** indicating good performance

		Sire breed											
		B	**S**	**Z**	**C**	**B**	**S**	**Z**	**C**	**B**	**S**	**Z**	**C**
		Birth weight				Weaning weight				Final weight (18 months)			
Dam breed	**B**	**	**	****		*	**	**		*	**	***	
	S	****	****	****		***	***	***		**	***	***	
	Z	*	**	*	***	***	***	***	****	***	***	***	****
		Tick resistance				Worm resistance				Heat resistance			
	B	*	**	****		**	*	***		*	***	***	
	S	**	*	****		**	*	***		**	***	***	
	Z	****	***	****	*	****	***	****	****	****	****	****	***
		Scrotal circumference				Calving success (wet cows)[a]				Calving success (dry cows)[a]			
	B	****	****	***		***		***		**		***	
	S	****	***	***			**	****			***	**	
	Z	**	*	*	*	***	***	**	*	****	****	***	****
		Days to calving[a]				Calf survival				Tenderness			
	B	***		**		**	****	**		****	***	**	
	S		**	***		****	****	****		***	***	**	
	Z	***	****	**	**	****	****	****	****	**	**	*	***

[a] recorded on the parental generation (dam genotypes)

As seen from the Table 24, no one breed excels in all characteristics of economic importance in the beef industry, and it is impossible to expect simultaneous improvement in all characteristics from intrapopulation selection (Cundiff *et al.* 1986). Hence, from this study it can be concluded that a properly designed crossbreeding programme can produce improved growth performance in beef cattle along with improvement in other economically important traits. Crossbreeding also results in progeny with better adaptation, relative to *Bos taurus* breeds, with resulting genotypes performing better even in tropical environments. The importance of including tick and worm resistance data when designing any breeding programme for tropical environments is well highlighted by the significant improvements in live weight gains of treated animals. Zebu and their crosses, with their resistance to heat, ticks, and worms and high direct and maternal additive effects for all growth traits, can form a dam line to be crossed with a taurine sire line to improve the growth performance of progeny. Taking into consideration the high fertility levels of taurine-indicine crosses, a crossbred dam line may also be useful to exploit maternal heterosis. Prediction of performance of untested genotypes based on the present estimates of direct and maternal additive and dominance effects can be very useful in making crucial decisions about breeding design, through avoiding waste of time and resources that come from inappropriate breeding decisions. Another implication of this study is the probable use of this crossbreeding performance data to augment existing purebred performance data, which then allows for multi-breed genetic evaluation.

As maintenance of some of the pure lines of taurine breeds in this tropical environment is difficult and also as Zebu breeds are not known for good fertility (though not proven in the present study), the production of composites by optimising the proportions of various breed groups through the use of crossbreeding parameters and economic weights can provide another alternative. The variability in direct breed and heterotic effects in various breed groups indicate a possibility of defining the optimal composite for this particular environment. As the number of traits that need to be considered for assessing total genetic value of a cross increases, the importance of deriving an optimal composite relative to systematic crossbreeding also increases. Further studies to derive economic weights for tick and worm egg counts at various levels of parasite challenge could provide more accuracy to the models of optimisation of breed proportions in tropical beef composites.

The parameters estimated in the present study can be used to develop decision support tools for predicting the performance of untested genotypes thereby guiding the breeding programme design for specific requirements. A strategic selection programme implemented thereafter in such a designed breeding programme is bound to derive favourable results. Fertility traits are least understood because of the problems associated with their recording and analysis and more so in extensive grazing systems. Fertility is a complex trait and renewed effort should be made to decipher the components of it to improve this most important trait. New technologies involving molecular genetic tools, identification of quantitative trait loci and genetic markers should be of great help in improving traits like fertility, disease resistance and meat quality.

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4. APPENDICES

4.1 Appendix 1.

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Evaluation of beef cattle genotypes and estimation of direct and maternal genetic effects in a tropical environment

1. Growth traits

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Abstract

Data from a crossbreeding experiment conducted during 1992 – 1997 involving 31 genotypes from tropically adapted British (B), Sanga derived (S), Zebu cross (Zx), Zebu (Z), and Continental (C) beef cattle breed groups were analysed to compare least squares means, direct and maternal genetic effects, and heterosis estimates for birth weight, weaning weight, yearling weight, final weight (18 months), and pre and postweaning average daily gain (ADG). The genotypes were regrouped as *Bos taurus* (B, S, C) and *Bos indicus* (Z, Zx) derived groups to enable the comparison of direct (dD) and maternal (mD) dominance effects among indicine (II), taurine – indicine (TI) and taurine (TT) crosses. Genotype, contemporary group (year of birth, season of birth and age of the dam), sex and genotype x sex interaction were significant (P<0.01) sources of variation for all the traits. Treatment to control parasites significantly (P<0.01) affected postweaning growth traits. In general, crossbred calves performed better than purebred calves. Z dam breeds resulted in lower birth weight, and Z sire breed, and S dam breeds resulted in heavier birth weights. For traits after birth, ZC, and ZC crosses with S and Z showed heavier weights and higher gains. Prior to weaning, males weighed significantly more and gained weight at a faster rate than females in most of the crossbreds. Weight gain was relatively low between weaning and yearling age.

Direct and maternal additive effects were estimated as a deviation from the British breed group mean for various traits. Direct additive effects of C, Z, and S were high and significantly different from the British mean for all the growth traits. Maternal additive effects of C were low and not significantly different from the British mean. Large negative maternal additive effects of Z and Zx caused lower birth weights of calves from Z and Zx dams. A decrease of maternal additive effect from weaning to final weight and preweaning to postweaning ADG was noticed. The magnitude of dD effects was higher in TI crosses than in II crosses for all the traits except for birth weight, indicating the advantage of *Bos taurus* x *Bos indicus* crosses. In TT crosses, dD was only significant for weaning weight ($P<0.01$) and preweaning ADG ($P<0.05$). Significant ($P<0.01$) and positive mD effects observed in TI crosses indicated a better maternal environment provided by crossbred dams. High correlation coefficient estimates (0.92 – 0.99) between least squares means and predicted means, observed for a set of F_1 genotypes, indicated the prediction of performance of untested genotypes with reasonable accuracy. The percent heterosis estimates were higher in Zebu x British breed crosses.

Additional keywords: additive effects, dominance effects, heterosis, crossbreeding, beef cattle

Introduction

Crossbreeding has evolved as an efficient breeding tool to improve productivity in tropical regions of Australia. The need to combine heat and parasite resistance traits with high growth rates in tropical climates has provided an economic incentive for crossbreeding. At a genetic level, crossbreeding systems provide a means to utilize both additive and nonadditive gene action simultaneously. There are many studies on crossbreeding in temperate regions (e.g. Long 1980, Gregory and Cundiff 1980), but research on crossbreeding in tropical climates is limited. Because of well established genotype x environment interactions in comparative growth rates (Frisch and Vercoe 1984; Arthur *et al.* 1994*a*) of various breeds, results obtained in one environment with a particular set of breeds cannot be generalised for all the environments. In tropical environments, stressors like high humidity and temperature, ecto- and endo-parasites, disease incidence, and seasonal nutrition affect the growth performance of various genotypes. Hence, in the present study, an attempt was made to compare the performance of various breeds and their crosses in a tropical environment with low to medium parasite challenge. In addition, estimation of genetic effects allows the prediction of performance of untested genotypes thereby helping the better design of a crossbreeding programme. Limited literature is available on crossbreeding genetic parameters in a tropical environment (Newman *et al.* 1998).

Hence, the objectives of this study are i) to compare various breed groups produced in a crossbreeding experiment based on their pre and postweaning growth traits, ii) to estimate direct and maternal additive and dominance effects of various breed groups involved in the study so as to enable the prediction of performance of various crosses, and iii) to estimate direct heterosis percentages in selected crosses thereby quantifying the improved performance through crossbreeding.

Materials and methods

This crossbreeding study was conducted during 1992 – 1997 at the National Cattle Breeding Station, ‘Belmont’, near Rockhampton, Queensland, Australia. The station is located 25 km north of the tropic of Capricorn, 40 km from the coast. The climate is dry tropical with unreliable wet seasons, with two-thirds of rainfall occurring between December and March. Winter (June to August) is the “dry” period of low nutrition. Cattle are subjected to numerous environmental stressors like high temperatures and humidity during summer, nutritional deficiency during the “dry” season, ecto-parasites (*Boophilus microplus* and buffalo fly, *Haematobia irritans exigua*), endo-parasites (gastro-intestinal helminths or worms, predominantly *Haemonchus*, *Cooperia* and

Oesophagostomum species), and periodic exposure to diseases (Bovine Infectious Kerato-conjunctivitis and Ephemeral fever). A more complete description of the background to this study was presented by Frisch and O'Neill (1998*a*, 1998*b*).

Breed pooling

Between 1992 and 1997, various breeds of African, European and Indian origin were crossed to compare various genotypes and identify the most productive genotypes. A total of 122 genotypes with the number of animals in each cross ranging from 1 to 338 were produced during this period. Only 71 genotypes with at least 10 progeny / genotype were included in the present analysis. Breeds were further regrouped based on their origins and similarities (Table 1) producing 31 genotypes for evaluation (Table 2). Belmont Adaptaur, Belmont Red, and Belmont BX are the synthetic breeds developed at Belmont by crossing and *inter se* mating for several generations to stabilise respective breed proportions in these lines (Frisch and O'Neill 1998*a*).

The grouping of Brahman and Boran together was based on their similarities and closeness as indicated in earlier studies on those populations (Frisch *et al.* 1997; Frisch and O'Neill 1998*a*). Tuli was grouped with Belmont Red because of their common Sanga *taurus* constitution and the Sanga derived group predominantly constituted Belmont Red in the present study. The British purebred group in this study consisted of the Belmont Adaptaur (Table 1), which is a tropically adapted selected line for tick resistance and 550-day liveweight. In this paper, B, S, Zx, Z, and C represent tropically adapted British, Sanga derived, Zebu cross, Zebu, and Continental breed groups respectively (Table 1). In crosses, the female parent is shown first with crossbred dams and sires shown in parentheses. Purebred performance information was not available for Boran, Tuli, Shorthorn, Charolais, or Simmental as they were only represented in crosses. Hence, ZZ represented only Brahman and Brahman x Boran cross, SS represented predominantly Belmont Red and a few Belmont Red x Tuli cross, and BB represented only Belmont Adaptaur. Shorthorns were only represented as sire breed of some crossbred dams. BB, SS, ZxZx, and ZZ were grouped as purebreds and from F_1 backcross onwards (Tables 2 and 3), reciprocals within dam breed group were pooled together.

Data

Live weights were recorded at birth, weaning, yearling age, and around 18 months of age (hereafter referred to as final weight). Average weaning age, yearling age, and age at final weight were 193, 372, and 524 days, respectively. Except during the 10-week breeding season, all cows grazed as a single herd. At the end of the breeding season the herd was divided based on the sex of calf. Steers and heifers were managed as separate cohorts after weaning and calves from each crop were allocated randomly within sex, genotype, sire and previous lactation status of the dam into either a treatment group or a control group. Animals in the treatment group were treated with anthelmintic to control gastro-intestinal nematodes regularly every 3 weeks from around 8 months of age to around 18 months of age. They were also inspected for cattle ticks (*Boophilus microplus*) and if ticks were present, all the treatment group animals were dipped in a plunge dip containing acaricide (Tactic, Hoechst, Australia). None of the dams was treated to control ecto- or endo-parasites. A detailed description about other management practices was given by Frisch and O’Neill (1998*a*, 1998*b*).

The 32 AX, 46 Bh, and 12 BX sires used during the entire study were selected for high estimated breeding value for 600-day live weight. The 40 HS sires used in the study were selected for high 550-day live weight and high tick resistance. Same sires were used to produce straightbred and crossbred calves in these breeds. The 18 Bo, 10 Tu, 4 Si, and 11 Ch sires were selected randomly. Number of sires within breed was maximised rather than number of progeny per sire as the primary aim was to estimate breed differences. Animals with missing information on date of birth, disputed parentage, with no proper breed identification and those animals whose weights (outliers) were affected by lantana (*Lantana camara* L.) poisoning were removed from the analyses. After all the edits, 2608 animals with birth weight, 2556 animals with weaning weight, 2460 animals with yearling weight, and 2440 animals with final weight records were used in the analysis and the number of animals in each breed group for each weight are given in Tables 2 and 3.

Statistical analysis

Data pertaining to birth weight, weaning weight, average daily gain (ADG) from birth to weaning, yearling weight, final weight, and postweaning ADG (ADG from weaning to final weight) were analysed using a univariate fixed effects model (model 1) in ASREML (Gilmour *et al.* 2001). Model 1 included the effects of genotype, contemporary group (consisting of year of birth, season of birth and age group of dam), sex, treatment (only for traits after weaning), and previous lactation status of the dam. Year of birth ranged from 1991 to 1996 and months of birth were regrouped into 3 seasons of birth (August – September, October – November and December – January). Age of dam at the time of calving was grouped into 3, 4, 5, and ≥ 6 years. Previous lactation status of the dam was categorised as wet cow, dry cow, cow with a dead calf and maiden heifer. Weaning weight, yearling weight, and final weight were adjusted for respective ages at the time of weighing by including age at weighing as a covariate. After testing the possible first order interactions for significance, the significant interaction effects were included in the analysis.

In model 2, genetic effects were partitioned in terms of direct additive, maternal additive, direct dominance and maternal dominance effects. These fractional coefficients of genetic effects of various genotypes are presented in Table 4. Because of the linear dependencies due to Σa_i (direct additive coefficients) =1 and Σm_i (maternal additive coefficients) =1, the full set of direct and maternal additive effects could not be estimated. Hence, the British breed group direct and maternal additive coefficients (aB, mB) were not included in the model and genetic components of other breed groups were estimated as a deviation from the British breed group (BB) mean. For the estimation of direct and maternal dominance effects, genotypes were further regrouped into *Bos indicus* x *Bos indicus* (II), *Bos taurus* x *Bos indicus* (TI) and *Bos taurus* x *Bos taurus* (TT) crosses. For the purpose of this regrouping B, S, and C were regarded as *Bos taurus* derived breeds and Z and Zx were regarded as *Bos indicus* derived breeds. Hence, the direct dominance (dD) effects for various genotypes were grouped as dD_{II}, dD_{TI} and dD_{TT} and maternal dominance (mD) effects were grouped as mD_{II}, mD_{TI} and mD_{TT}. This was necessary because of lack of information on all the reciprocals. The genetic effects were estimated as partial regression coefficients by treating the fractional coefficients as continuous variables in the analysis using the following model (model 2) with ASREML (Gilmour *et al.* 2001):

$$Y_{ij} = \mu + F + b_1 A + b_2 M + b_3 dD + b_4 mD + e_{ij}$$

Where, Y_{ij} is j^{th} observation on the i^{th} animal; μ is least squares mean of the British breed group (BB); F are all the significant fixed effects and covariates included in model 1; b_1 are partial regression coefficients representing direct additive effects of S, Zx, Z, and C expressed as a deviation from the BB mean; b_2 are partial regression coefficients representing maternal additive effects of S, Zx, Z, and C expressed as a deviation from the BB mean; b_3 are partial regression coefficients representing direct dominance effects of II, TI, and TT crosses; b_4 are partial regression coefficients representing maternal dominance effects of II, TI, and TT crosses; A and M represent the fractional coefficients of direct and maternal additive effects for S, Zx, Z, and C breed groups and dD and mD represent the fractional coefficients of direct and maternal dominance effects for II, TI, and TT crosses.

The predicted means of F_1 genotypes (as an example) were estimated from direct and maternal additive and dominance effects, and fractional coefficients of various breed groups as: Predicted mean = British breed group least squares mean + (direct additive effect x A fractional coefficient) + (maternal additive effect x M fractional coefficient) + (direct dominance effect x dD fractional coefficient) + (maternal dominance effect x mD fractional coefficient). The correlations between least squares means for each trait obtained by model 1 and predicted means derived from genetic effects obtained by model 2 were estimated to evaluate the accuracy of predictions.

Heterosis estimates were only derived for those F_1 crosses where reciprocals existed. Heterosis was estimated using the least squares means for each trait as a deviation of the F_1 mean from the parental population mean and expressed as a percentage of the parental population mean.

Results

Genotype differences

Analysis of variance showed that all traits were significantly ($P<0.01$) affected by genotype, contemporary group, sex, and genotype x sex interaction. Treatment was a significant ($P<0.01$) source of variation for traits after weaning. Genotype x treatment interaction was significant ($P<0.01$) only for postweaning ADG. The effect of treatment and its interaction is dealt separately with the information on tick and worm counts in another paper (Prayaga 2003). Previous lactation status of the dam was significant ($P<0.01$) for all traits except postweaning ADG. Least squares means for various traits along with their rankings within the trait are presented in Tables 2 and 3. These genotype rankings were only indicative of the respective position of the genotype within the trait of interest and were not based on significant differences. Although the least significant difference was computed for any pairwise comparison (Tables 2 and 3), based on the overall standard error of difference, it should be noted that only preplanned comparisons (with respective standard errors of difference) should be made, because of the large number of possible comparisons. Sex differences in each of the breed groups expressed as a deviation of female mean from male mean are also presented (Tables 2 and 3). However, as the sexes were reared separately after weaning, the differences between sexes were influenced by unexplained environmental factors not included in the model. Hence postweaning sex differences are not discussed.

The overall least squares mean for birth weight was 33.7 kg (range 29.4 to 38.1 kg) with male calves weighing 2.4 kg more than females. Birth weight in SZ was heaviest followed by S(ZC) and (ZC)Z. Lightest birth weights were recorded in Z(BS), ZZ, ZZx, and ZB. Z dam breeds produced calves with lighter birth weights and S dam breeds produced heavier birth weights. This was further substantiated by SS having the heaviest birth weight among purebreds. When Z was used as a sire breed rather than a dam breed, birth weights increased. Within F_1s, Zebu dams had calves with lower birth weights except in ZC. Birth weights were generally heavier wherever ZC was used as either a dam or a sire. Male calves of SZ weighed 5.8 kg more than females at birth. Very large sex differences in birth weight were also observed in (BS)Z, SB and ZxZ.

The overall mean weaning weight was 194 kg (range 157 to 216 kg) and male calves were 17 kg heavier than female calves. Mean preweaning ADG was 832 g/day (649 to 938 g/day) with males gaining 75 g/day more than females. Ranking of breed groups changed significantly at weaning relative to their ranking at birth. ZC and ZC crosses with S and Z were significantly heavier at weaning and had higher preweaning ADG. ZC ranked 12th for birth weight but was the heaviest group at weaning. BB were lightest at weaning and had the lowest preweaning ADG. All other purebreds (SS, ZxZx, and ZZ) were also slightly below the mean weaning weight and had a slower preweaning ADG than the overall mean. BZ and BS (i.e. crossbred calves reared by British dams) had low weaning weights and preweaning ADG. Calves reared by Zebu crossbred dams in F_1 backcrosses and three breed crosses performed well for preweaning growth traits. Males were significantly heavier and grew significantly faster than females in most crossbreds. There was no difference between sexes in ZC, which were heaviest at weaning and grew fastest until weaning.

The overall mean yearling weight was 226 kg (range 182 to 254 kg). The overall weight gain from weaning to yearling age was 32 kg (226 – 194 kg) in 179 days (difference between mean yearling and weaning ages) at around 176 g/day. ZC, (ZC)S and (ZC)Z were still the heaviest groups at yearling age and BB was still the lightest. BS and (ZxB)B with $\geq$ 75% *Bos taurus* contribution were also relatively light at yearling age. The overall mean final weight was 324 kg (range 263 to 368 kg). The heaviest and the lightest genotypes at weaning (ZC and BB respectively) ranked the same at final weight. C breed crosses with Z and S attained heavier weights than crosses involving tropically adapted British breeds. Among F_1s, BS and SB (100% *Bos taurus*) performed poorly. However, BZ and ZB performed relatively better as they benefited from significant *Bos taurus* x *Bos indicus* heterosis levels. In F_1 backcrosses, (ZxB)B had the lightest final weight. Better performance of 3 breed crosses and F_1 x F_1 crosses also indicated the expression of heterosis.

The mean postweaning ADG over all genotypes was 394 g/day (range 319 to 459 g/day). ZC recorded the fastest postweaning ADG, followed by (ZZx)S. The slowest postweaning ADG was observed in the genotypes with the highest *Bos taurus* content (i.e., (ZxB)B, BB, BS, SB, and (ZB)B). The rankings for postweaning ADG were different to that of the final weight in some genotypes. In BZ, in spite of a higher postweaning growth rate, final weight was only around the overall mean performance, suggesting a poor maternal environment of the British dam still affecting weights at 18 months of age. In (ZC)Z, postweaning ADG was only at an average level (403 g/day), but final weight was significantly ($P<0.05$) above the mean performance of all genotypes.

Genetic effects

Direct and maternal genetic effects of various breed groups for the traits under study are presented in Table 5. The direct additive effect of the C (aC) breed group as a deviation from the British (BB) mean was significant ($P<0.01$) and highest in all growth traits. The direct additive effects of Z (aZ) and S (aS) were also significantly different from BB mean ($P<0.01$), but the direct additive effect of Zx (aZx) was only significant after weaning. The aC was almost double the aZ in all traits except for postweaning ADG. The aZ and the aS were similar from weaning to yearling age, but slightly higher values for Z than S were obtained for final weight and postweaning ADG. The aZx was lower than the aZ for all traits. Maternal additive effects of the C (mC) breed group, as a deviation from BB mean, were low and insignificant ($P>0.05$) for all traits. For birth weight, maternal additive effects of Z (mZ) and Zx (mZx) were significantly ($P<0.01$) negative compared to BB mean. As expressed as a deviation from BB mean, the maternal additive component of S (mS) was not significant after weaning and mZx was not significant after yearling age. The mZ was significant up to final weight ($P<0.01$) but not significant for postweaning ADG. A decrease in the maternal additive components from weaning to final weight and from preweaning ADG to postweaning ADG was observed in S, Z and Zx.

Direct dominance effects were significant for all the traits in II and TI crosses, which indicated the presence of significant heterosis in the crosses under study. The magnitude of direct dominance effects in TI crosses was more than double that of II crosses for all the traits, except for birth weight. TT crosses resulted in significant direct dominance effects only for weaning weight ($P<0.01$) and preweaning ADG ($P<0.05$).

Maternal dominance effects were only significant ($P<0.01$) in TI crosses for all the traits under study, with a negative mD_{TI} effect for postweaning ADG. In TT crosses, mD was significant ($P<0.05$) for preweaning ADG and yearling weight; in II crosses, mD was significant ($P<0.05$) and positive for yearling weight and postweaning ADG. These results reflect the importance of breed selection in maternal lines to exploit maternal heterosis.

The predicted means of F_1 crosses for all the traits under study are presented in Table 6. High correlation coefficient estimates (0.92 to 0.99) between least squares means of F_1 crosses derived from model 1 and predicted means of F_1 crosses derived from genetic effects (model 2) were observed.

Heterosis

Percent heterosis for selected two breed group crosses (F_1s), where reciprocals existed, are presented in Table 7. Heterosis percentages were positive in all crosses. The percent heterosis values ranged from 2.1 to 8.2% for birth weight, 2.2 to 8.5% for weaning weight, 1.5 to 8.0 % for preweaning ADG, 2.8 to 13.1% for yearling weight, 1.3 to 12.7 % for final weight and 1.7 to 18.8 % for postweaning ADG. High and significant heterosis values were obtained in Z and B crosses at all weights.

Discussion

Genotype differences

The main purpose of crossbreeding in a tropical environment is to improve the performance of animals under stressful environmental conditions by complementing the desirable genes from both parental breeds. Significant genotype differences in the present study emphasise the need for proper selection of breeds in crossbreeding programmes by taking into consideration genetic complimentarity of both sire and dam breeds and environmental adaptation of the resulting genotype.

Lower birth weights of Zebu straightbreds as well as lower birth weights in crosses where the Zebu breed is used as a dam reinforces the view that the Brahman (Roberson *et al.* 1986) dams produce smaller calves. The effect of lower birth weight of Z is evident from the comparison of SZ (38.1 kg) and its reciprocal ZS (31.3 kg) or BZ (36.7 kg) and its reciprocal ZB (30.7 kg). Hence, in stressful tropical conditions where lower birth weights may be desirable for calving ease, Z breeds are better suited as dam breeds. The lower birth weight effect of Z is overridden when crossed with taurine breeds as ZC or ZS dams produced relatively heavier calves at birth. The very large sex differences in birth weight observed for Z sired crosses are comparable to the large sex differences in birth weight between Brahman- sired and Tuli- sired calves observed in subtropical areas of the USA (Chase *et al.* 2000). As heavier birth weights are associated with production problems (dystocia, calf loss, reduced calf performance) for beef producers, cross breeding programmes should be aiming to maintain medium birth weight ranges.

Changes in the rankings of genotypes in weaning weight and preweaning ADG relative to birth weights are attributed to the differences in maternal abilities of dam breed groups and the differences in expression of additive genetic potential of calves under stressful climatic conditions. The heaviest weaning weight and the highest preweaning ADG achieved by C sired calves (ZC) is comparable to Charolais- sired calves ranking highest in birth weight, average daily gain and weaning weight in an experiment involving Angus, Hereford and Charolais crosses (Dillard *et al.* 1980). This reflects the heavier mature size of Continental breeds contributing to heavier weaning weights and faster daily gains in their progeny compared to other taurine breeds used in the study. High phenotypic correlation estimate of 0.91 (Gregory *et al.* 1992) between milk yield and weaning weight suggest that the weaning weights may be highly influenced by the dam's milk yield. Hence, lower weaning weights and preweaning ADG observed in calves from the British dams can be attributed to their low milk producing ability under tropical environments (Lamond 1973). Even in temperate environments of the USA (Gregory *et al.* 1992) and Australia (Meyer 1992), lower weaning weights in purebred Hereford calves were associated with low milk production of Hereford dams among temperate breeds.

Lower weight gains obtained between weaning and yearling age are in agreement with the findings of Mackinnon *et al.* (1991) in tropical Australia. Growth between weaning and yearling weights is crucial in tropical environments because the weaning stress is coupled with exposure of calves to parasite burdens. Also, in tropical and subtropical environments in Australia, this period between weaning to yearling age coincides with the traditional "dry" season and hence calves would either maintain their weaning weights or in some cases even lose weight between weaning and yearling ages. The parasite load was perceived to be low to moderate in the present study and one half of the animals were treated. However, a significant treatment effect showed that treated animals grew better than untreated animals over all genotypes for all postweaning growth traits, emphasising the importance of postweaning environment on growth.

The differences in rankings between final weight and postweaning ADG lead me to believe that some of the genotypes (like ZZ, BZ) may be growing faster in this period and may compensate for slower preweaning growth. In tropical environments, two phases of postweaning growth namely dry season growth (measure of adaptation when feed quality is low and parasite burdens particularly worms are high) and wet season growth (*ad libitum* good quality feed that enables the animals' immune system to cope more efficiently with the stressors) are evident. However, the net combined efficiency of postweaning growth in these two phases is of commercial importance and hence in the present study only a single postweaning ADG from weaning to final weight is considered.

In the present study, conditions may not have been typical of normal tropical climate. Lower parasite burdens and treatment of half of the animals against ticks and worms in the postweaning period boosted the overall performance of certain genotypes like ZC. Besides, the use of C breeds at higher proportions in crossbreds may improve the growth performance, but it may affect the overall productivity because of their excessive maintenance requirements due to heavier mature sizes. This is of concern when most or all of the heifer calves are to enter the breeding cow herd. Because of this, imposing an upper limit on the proportion of C breeds may be a good idea while optimising cattle composites for tropics. A clearer understanding of the breed contribution to growth performance can be derived from comparing additive and maternal genetic affects of various breed groups.

Genetic effects

The reasons for differences in the performance of various crossbred genotypes are the differences in breed additive, maternal additive, direct dominance, maternal dominance and epistatic effects. The model of estimation of genetic effects has the advantage of using information from all available genotypes in the study. Hence, these genetic effects are extremely useful in explaining the differences observed in the least squares means derived from model 1 for various genotypes.

The relatively larger birth weights observed for Zebu-sired calves can be explained by the large aZ for birth weight. Gregory *et al.* (1979) also reported that Brahman- sired calves were heaviest in a temperate environment of Nebraska and noted that crosses had significantly higher level of calving difficulty. The significant and negative mZ for birth weight explains the lower birth weights in Zebu crosses with Z as dam, which are large enough to overcome the positive direct heterosis effect in crossbreds. There are several reports of negative Brahman maternal additive effects for birth weight (Table 8). The lower birth weights obtained by purebred ZZ are due to the higher negative mZ overriding the positive aZ effect. This combination of large positive direct additive and large negative maternal additive effects of Zebu breeds for birth weight can be exploited by careful designing of breeding programmes depending on the need and environmental conditions.

The positive mZ is comparable to the highly positive and significant Brahman maternal additive effect in a sub-tropical tick-free environment (Arthur *et al.* 1994*b*) for preweaning ADG and weaning weight in low quality pastures. However, the negative Brahman additive effect (as a deviation from Hereford mean) for weaning weight and preweaning ADG (Roberson *et al.* 1986) and insignificant Brahman maternal additive effect (as a deviation from Hereford mean) for preweaning ADG and weaning weight (Arthur *et al.* 1999) are in contrast to the present finding of positive and significant additive effects for Zebu, which may be explained by the differences in environments between studies. The environments in Roberson *et al.* (1986) and Arthur *et al.* (1999) are tick free subtropical environments while the present results are from a low to moderate tick infested tropical environment. Though the high direct additive effect of Charolais for preweaning ADG observed by Franke *et al.* (2001) in a subtropical environment can be compared to aC in the present study, the higher direct additive effect of Hereford relative to Brahman contradicts the present results. This again highlights the environmental influence on performance of various genotypes and stresses the need for assessing the genotypes in the environment of interest because of the possibility of reranking of breed groups for crossbreeding parameters.

The general perception of the Brahman's contribution to the commercial beef cattle production is their favourable maternal influence in early calf growth and their advantage in adaptation to tropical and subtropical environments (Roberson *et al.* 1986). The present study supports this perception as evidenced by highly significant ($P<0.01$) maternal additive effects of Z and Zx for weaning weight and preweaning ADG. Significant and high mZ and mZx for weaning weight indicate greater maternal ability of dams in the Z and Zx breed groups, which in turn reflect on their good milk producing ability. Reports of high milk production of Brahman and Brahman crosses in temperate (Cundiff *et al.* 1986) and tropical (Lamond 1973) environments support this inference. The similarity of mZ and mZx further justifies the grouping of Z and Zx into an indicine group for the estimation of direct and maternal dominance effects in the present study.

Though maternal additive effects are only expected to be significant up to weaning, there may be some carry over effect to yearling weight. However, it would not be expected that they would persist to final weight. The significant mZ for final weight recorded in the present study is comparable to the observation made by Meyer (1992) that fitting the maternal effect increased the log likelihood significantly in an animal model for final weight of Zebu crosses, implying that in Zebu crosses maternal effects are important even for final weight. This shows the prolonged influence of maternal effects in Zebu cattle. Though C pure breeds were not tested for their performance in the present study, their performance is expected to be poor because of their lack of resistance to stressors of tropical environments similar to other taurine breeds (Frisch and O'Neill 1998*b*). However, because of their very large direct additive effect on growth, their crosses with Z dam breeds with 25 – 50% C breed group proportions perform well due to complimentarity (Tables 2 and 3).

The significant direct dominance effects in the present study indicated the crossbred advantage over straightbreds. The lack of significance in direct dominance effects in crosses among taurine breeds for birth weight and postweaning growth traits is due to the genetic similarities among taurine breeds giving little scope for expression of non-additive gene action. Significant and high direct and maternal dominance effects in TI crosses emphasises that hybrid vigour is better exploited by crossing the breeds of distant relationship such as those of taurine and indicine origins. Cundiff *et al.* (1986) also demonstrated the significant contribution of *Bos indicus* breeds even in temperate climates through crossbreeding, as heterosis for growth traits was greatest for *Bos taurus* x *Bos indicus* crosses. This is further substantiated by the lower magnitude of direct dominance effects in either II or TT crosses in the present study. Franke *et al.* (2001) reported significant direct heterosis effects for Brahman x Charolais and Brahman x Hereford crosses for birth weight, average daily gain and 205 day weight in a subtropical environment of USA and stated that these heterosis effects were significantly greater than those not including Brahman in the cross. This is comparable to the high and significant dD_{TI} components in the present study. The positive and significant mD_{TI} parameters for weaning weight and preweaning ADG in the present study indicate that taurine x indicine crossbred dams provide a better maternal environment to their calves than purebred or taurine crossbred or indicine crossbred dams. These mD_{TI} effects are in agreement with Roberson *et al.* (1986) and Arthur *et al.* (1994*b*) and refer to the improved performance in progeny by using crossbred dams compared to purebred dams.

The additive and maternal effects of Z relative to the British mean and the direct and maternal effects of TI crosses are compared with the corresponding estimates from the literature (Table 8) based on the Brahman and Hereford breeds in various environments. Across all the environments, positive direct additive and negative maternal additive effects of Zebu as a deviation from British breeds for birth weight are quite evident. However, aZ and dD_{TI} effects for birth weight in temperate climates are not significant. For weaning weight and preweaning ADG, the relative contribution of the Zebu additive effect gradually shifted from a significantly high positive effect in a tropical climate to a significantly high negative effect in a temperate climate. In subtropical climates, the contribution of direct additive Zebu effect varied from insignificant to significantly negative. The maternal additive effect of Zebu was not observed in temperate climates, though it was significantly positive in subtropical US studies, confirming the importance of Zebu breeds as maternal lines.

The very large positive direct dominance effects in TI crosses across all the environments for weaning weight and preweaning ADG (Table 8) emphasises the importance of crossing *Bos taurus* and *Bos indicus* breeds irrespective of environment. Even in sub-tropical and temperate climates, TI crosses are expected to perform well because of the large dominance effects overriding the negative or non significant additive and maternal effects of Zebu breeds. The significant mD_{TI} effect even in subtropical climates indicates the wide range adaptability of TI crossbred dams. Olson *et al.* (1991) found the growth advantage of *Bos taurus* x *Bos indicus* crossbred calves over *Bos taurus* x *Bos taurus* calves in sub-tropical (Florida) to be 3 times that in temperate (Nebraska) climates. This difference may be primarily due to the differences among breeds in their direct and maternal additive effects in various environments (Table 8).

It is important to note that for postweaning growth traits, indicine cross (II) dams performed well in the present study. The significant and positive mD_{II} effect on postweaning ADG indicate that indicine crossbred dams have a positive effect on postweaning growth rate of their calves. Compensatory growth (Arthur *et al.* 1994*b*) observed in postweaning periods in crosses where there was slow preweaning growth rate could be the reason for the progeny of II crosses having high maternal dominance effect for postweaning ADG. Compensatory growth as the causative effect is further justified by the similarity of mD_{TI} and mD_{II} effects for final weight. However, because of lower direct dominance effects in II crosses compared to TI, the overall performance of progeny resulting from II crosses will be lower than TI crosses. These results suggest that a dam line of indicine crosses mated to taurine sire breeds may result in fast growing progeny because of the optimum exploitation of additive and non additive genetic effects for growth traits. The inclusion of traits such as fertility in the model for evaluation may change this conclusion.

The genetic effects in the present study included only additive and dominance effects. Epistatic effects were ignored, assuming that after fitting direct and maternal additive and dominance effects, the contributions of epistasis and linkage to the genotype differences would be insignificant. Kinghorn and Vercoe (1989) showed that because of the colinearity of dominance and epistatic coefficients, whichever pair of effects, either direct and maternal dominance or direct and maternal epistasis, is fitted in the model, the second tends to add little information. The high correlation coefficients between least squares means obtained by model 1 and the predicted means derived from the genetic effects obtained from model 2 (Table 6) indicate that these genetic effects can be used with reasonable accuracy for the estimation of predicted performance of genotypes not tested in the study. This also emphasises that exclusion of epistatic effects in the model did not greatly affect the prediction of performance. Dillard *et al.* (1980) and Robison *et al.* (1981) also found that omission of epistatic effects in the model for the estimation of genetic effects did not significantly affect the accuracy of prediction of performance.

Despite the above, Arthur *et al.* (1999) advocated that in developing models to predict the performance of untested genotypes, additional genetic effects like epistasis should be included, if the data structure allows. There is also some evidence to suggest that epistatic effects are important in crosses between Sanga and other breeds (unpublished data). This result, derived from the observed recombination losses from F_1 to F_2 generations, is more pronounced in fertility traits than growth traits. This may be also true in complex crosses, where the predictions may not be accurate because of epistatic loss in performance resulting from breakdown of favourable interactions between loci built up through selection. Demeke *et al.* (2003) also stated that the breakdown of the positively associated epistatic genes of parental origin seem to be the main cause of the lower growth performance in later generations of *Bos taurus* x *Bos indicus* crosses and hence recommended the inclusion of epistatic effects in crossbreeding models. In the present study, estimation of effects may also be affected by the lack of information on specific direct and maternal dominance effects. Importantly, the genetic effects derived in this analysis are specific to this tropical environment with low parasite load and extrapolation and prediction of performance of any breed crosses from these crossbreeding parameters, for e.g. purebred performance of Charalois in tropical climate would lead to wrong predictions. However, when necessary precautions such as including 25% tropically adapted genes in subtropical climates and up to 50% tropically adapted genes in tropical environments are taken, these parameters may apply universally for prediction of growth performance.

Heterosis

Bos indicus cattle are better adapted and more resistant to ticks and worms (Frisch and O'Neill 1998b), while *Bos taurus* cattle have higher growth rates in less stressful environments (Arthur *et al.* 1994*a*). Crosses between these distinctly different breed groups result in hybrid vigour for growth and adaptive traits such as resistance to ticks and worms (Frisch and O'Neill 1998a, 1998b). In beef cattle, direct heterosis effects are generally in the range of 1 - 11% for birth weight, 3 - 16% for weaning weight, 3 - 8% for preweaning ADG, 2 - 7% for yearling weight, 1 - 8% for post-yearling weight, and 2 - 11% for postweaning ADG (Long 1980). The present estimates of direct heterosis fall in this range. Higher heterosis estimates are observed for the postweaning growth traits in Z and B crosses in the present study. Gregory *et al.* (1992) also reported greater (two fold) heterosis from crosses of *Bos taurus* with *Bos indicus* breeds than crosses among *Bos taurus* breeds even in temperate environments. These higher heterosis estimates achieved for Zebu / British crosses were despite the fact that the British breed group recorded the lowest additive genetic effects for growth traits in the present environment. This substantiates the earlier conclusion that when tropically adapted genes (Zebu) are present at around 50% level in tropical environments, the high direct dominance effects would influence growth by overriding the low additive and maternal genetic effects of one of the parental breeds.

Conclusions

No one breed excels in all characteristics of economic importance in the beef industry, and it is impossible to expect simultaneous improvement in all characteristics from intrapopulation selection (Cundiff *et al.* 1986). However, from this study it can be concluded that a properly designed crossbreeding programme can produce improved growth performance in beef cattle while balancing the improvement in other economically important traits. Zebu and their crosses, with their resistance to heat, ticks, and worms and high direct and maternal additive effects for all growth traits, can form a dam line to be crossed with a taurine sire line to improve the growth performance of progeny. As maintenance of some of the pure lines of taurine breeds in this tropical environment is difficult and also as Zebu breeds are not known for good fertility, the production of composites by optimising the levels of various breed groups and capping the maximum proportions of certain non adapted taurine breeds can be another alternative. Prediction of performance of untested genotypes based on the present estimates of direct and maternal additive and dominance effects can be very useful in making crucial decisions about breeding design, avoiding waste of time and resources that come from inappropriate breeding decisions. The genetic effects estimated here along with the economic weights for various traits also aid in optimising the breed proportions in composite formation. Another implication of this study is the probable use of this crossbreeding performance data to augment existing purebred performance data, which then allows for multi breed genetic evaluation. Significant heterosis estimates prompt the selection of genetically distant sire and dam lines to exploit maximum hybrid vigour.

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Table 1. Breed group formation from the breeds involved in the study

Breed group name	Dam breeds	Sire / Sire of the dam breeds
Bos taurus derived		
Tropically adapted British (B)	Belmont Adaptaur (HS) (Synthetic breed of ½ Hereford, ½ Shorthorn)	HS Shorthorn*
Sanga derived (S)	Belmont Red (AX) (Synthetic breed of ½ Africander, ¼ Hereford, ¼ Shorthorn)	AX, Tuli (Tu)
Continental (C)	-	Charolais (Ch), Simmental (Si)
Bos indicus derived		
Zebu (Z)	Brahman (Bh)	Brahman (Bh), Boran (Bo)
Zebu cross (Zx)	Belmont Brahman cross (BX) (Synthetic breed of ½ Brahman, ¼ Hereford, ¼ Shorthorn)	BX

*only represented as the sire breed of crossbred dams

Table 2. Least squares means and standard errors of preweaning growth traits for various genotypes under study along with rankings of genotypes given in parentheses and sex differences

Differences between means of >1.8kg, >8.2kg, >39.6g/day are significant ($P<0.05$) for birth weight, weaning weight, and preweaning average daily gain respectively. Breed group in genotype as given in Table 1 with female breed given first in the crosses and crossbred dams and sires identified in parentheses, M-F is mean deviation of female from male

Genotype	N	Birth weight (kg)	M-F	N	Weaning weight (kg)	M-F	Preweaning ADG (g/day)	M-F
Over all	2608	33.7±0.2	2.4**	2556	194±1.0	17**	832±4.9	75**
Purebred								
BB	316	31.9±0.3 (24)	2.4	302	157±1.5 (31)	13*	649±7.0 (31)	53
SS	231	36.3±0.3 (6)	3.1*	225	188±1.6 (24)	11	786±7.7 (27)	44
ZxZx	58	31.5±0.6 (25)	1.1	56	184±2.9 (27)	8	793±13.9 (25)	45
ZZ	274	30.4±0.3 (30)	3.1*	265	187±1.5 (25)	20**	815±7.2 (23)	93**
F_1								
BS	46	32.9±0.7 (20)	1.7	46	170±3.2 (30)	11	706±15.4 (30)	43
SB	22	36.7±1.1 (4)	5.3**	21	182±5.0 (28)	10	750±24.0 (28)	24
BZ	92	36.7±0.5 (5)	2.6*	92	178±2.3 (29)	7	733±11.2 (29)	15
ZB	116	30.7±0.5 (28)	0.1	114	195±2.1 (17)	16**	849±10.0 (12)	87**
SZ	137	38.1±0.4 (1)	5.8**	137	196±2.0 (14)	19**	822±9.4 (21)	72*
ZS	179	31.3±0.4 (27)	0.2	176	199±1.8 (11)	12*	870±8.4 (8)	65*
ZZx	52	30.4±0.7 (29)	1.7	51	188±3.1 (23)	12*	814±15.0 (24)	63*
ZxZ	102	34.1±0.5 (14)	4.8**	102	193±2.2 (21)	23**	830±10.7 (19)	100**
ZxS	58	31.4±0.6 (26)	2.3	56	193±2.9 (20)	15**	839±14.0(16)	67*
ZC	93	34.4±0.5 (12)	-1.7	92	216±2.3 (1)	5	938±11.0 (1)	32
F_1 backcross								
(ZB)B	56	32.1±0.6 (23)	0.4	56	196±2.9 (12)	20**	844±14.1 (13)	99**
(ZB)Z	120	35.4±0.5 (9)	3.4**	120	203±2.1 (9)	19**	867±10.1 (9)	73*
(ZS)S	35	33.5±0.8 (17)	-0.1	35	204±3.6 (6)	18**	879±17.3 (6)	93**
(ZS)Z	64	34.3±0.6 (13)	1.6	63	203±2.9 (8)	16**	875±13.7 (7)	74**
(ZZx)Z	21	32.1±1.1 (22)	3.2*	20	194±5.1 (18)	15*	833±24.6 (18)	53
(ZxB)B	49	33.4±0.7 (18)	4.3**	49	186±3.2 (26)	28**	792±15.3 (26)	118**
(ZC)Z	43	36.8±0.7 (3)	4.3**	42	213±3.3 (3)	15*	911±15.8 (3)	65*
3-breedcross								
(BS)Z	20	36.1±1.0 (7)	5.4**	20	195±4.7 (15)	30**	825±22.7 (20)	119**
(ZB)S	116	33.7±0.5 (16)	1.4	114	206±2.1 (4)	24**	892±10.2 (4)	110**
(ZZx)S	35	32.8±0.8 (21)	2.9*	34	195±3.8 (16)	15*	840±17.7 (14)	58*
(ZC)S	28	35.8±0.9 (8)	2.8*	28	215±4.0 (2)	23**	922±19.2 (2)	102**
Z(BS)	41	29.4±0.7 (31)	1.3	39	190±3.5 (22)	20**	836±16.5 (17)	100**
S(ZC)	31	37.0±0.9 (2)	4.1**	30	203±4.0 (7)	20**	860±19.0 (10)	88**
F_1 x F_1								
(ZB)(SZ)	49	33.4±0.7 (19)	1.9	46	200±3.3 (10)	13*	860±15.6 (11)	53
(ZS)(SZ)	65	33.7±0.6 (15)	0.4	65	196±2.8 (13)	17**	840±13.6 (15)	85**
(ZS)(ZC)	33	34.5±0.9 (11)	2.0	33	204±3.9 (5)	26**	881±18.8 (5)	121**
(BS)(ZC)	26	34.7±0.9 (10)	3.6**	26	193±4.1 (19)	24**	816±19.9 (22)	97**

*$P<0.05$, **$P<0.01$

Table 3. Least squares means and standard errors of postweaning growth traits for various genotypes under study along with rankings of genotypes given in parentheses and sex differences

Differences between means of >10.2kg, >12.5kg, >26.3 g/day are significant (P<0.05) for yearling weight, final weight, and postweaning average daily gain respectively. Breed group in genotype as given in Table 1 with female breed given first in the crosses and crossbred dams and sires identified in parentheses, M-F is mean deviation of female from male

Genotype	N	Yearling weight (kg)	M-F	N	Final weight (kg)	M-F	Postweaning ADG (g/day)	M-F
Over all	2460	226±1.3	5**	2440	324±1.5	35**	394±3.2	39**
Purebred								
BB	271	182±1.9 (31)	3	270	263±2.3 (31)	30**	319±4.7 (30)	26
SS	221	221±2.0 (23)	7	217	316±2.4 (25)	25**	388±5.0 (21)	24
ZxZx	52	215±3.7 (27)	-6	50	312±4.5 (27)	4	384±9.5 (23)	-16
ZZ	251	218±1.9 (26)	15*	251	320±2.3 (23)	45**	404±4.7 (12)	53**
F_1								
BS	46	204±3.9 (30)	7	46	290±4.7 (30)	19*	365±9.9 (27)	8
SB	20	214±6.2 (28)	-33**	20	297±7.5 (28)	22*	354±15.7 (29)	23
BZ	89	219±2.9 (25)	0	87	322±3.6 (21)	17	436±7.5 (3)	24
ZB	110	233±2.6 (9)	9	108	334±3.1 (8)	32**	423±6.6 (6)	29
SZ	131	233±2.4 (10)	11	131	339±3.0 (6)	36**	432±6.2 (5)	38*
ZS	169	236±2.2 (6)	1	164	342±2.7 (4)	24**	433±5.6 (4)	22
ZZx	50	219±3.9 (24)	3	50	320±4.7 (22)	15	402±9.8 (14)	-7
ZxZ	100	227±2.8 (15)	13	99	328±3.4 (15)	37**	406±7.0 (10)	23
ZxS	52	224±3.6 (19)	13	52	323±4.4 (20)	36**	391±9.2 (18)	47**
ZC	90	254±2.8 (1)	-4	90	368±3.4 (1)	15	459±7.2 (1)	13
F_1 backcross								
(ZB)B	56	221±3.6 (21)	5	56	313±4.4 (26)	34**	355±9.2 (28)	25
(ZB)Z	118	231±2.6 (13)	8	118	325±3.2 (18)	36**	369±6.6 (25)	30
(ZS)S	35	235±4.4 (7)	-4	35	335±5.4 (7)	33**	399±11.3 (15)	31
(ZS)Z	63	231±3.5 (12)	1	63	333±4.2 (9)	46**	396±8.8 (16)	74**
(ZZx)Z	18	226±6.7 (16)	-24**	17	327±8.8 (16)	32**	418±18.7 (7)	54**
(ZxB)B	49	205±3.9 (29)	9	48	291±4.8 (29)	38**	318±10.0 (31)	8
(ZC)Z	42	242±4.0 (3)	3	42	344±4.9 (3)	25**	403±10.5 (13)	16
3-breedcross								
(BS)Z	19	237±5.9 (5)	18*	19	331±7.1 (11)	75**	414±14.9 (8)	128**
(ZB)S	112	232±2.6 (11)	14	111	330±3.2 (13)	41**	375±6.7 (24)	29
(ZZx)S	35	238±4.5 (4)	11	35	340±5.5 (5)	48**	441±11.4 (2)	86**
(ZC)S	27	247±5.0 (2)	10	27	349±6.0 (2)	37**	394±12.7 (17)	44*
Z(BS)	39	222±4.2 (20)	2	39	324±5.1 (19)	42**	407±10.7 (9)	51**
S(ZC)	29	225±4.9 (18)	9	29	330±5.9 (12)	41**	390±12.4 (20)	42*
F_1 x F_1								
(ZB)(SZ)	44	233±4.0 (8)	10	44	329±4.9 (14)	46**	388±10.2 (22)	66**
(ZS)(SZ)	64	221±3.5 (22)	5	64	316±4.2 (24)	37**	366±8.9 (26)	37*
(ZS)(ZC)	32	230±4.8 (14)	22**	32	332±5.9 (10)	60**	391±12.3 (19)	89**
(BS)(ZC)	26	225±5.1 (17)	11	26	325±6.1 (17)	52**	405±12.8 (11)	71**

* P<0.05, ** P<0.01

Table 4. Fractional coefficients of genetic effects (breed additive, maternal additive, direct dominance and maternal dominance) for various genotypes in the study.

a-additive, m-maternal, dD-direct dominance, mD –maternal dominance, II – indicine breed crosses, TI – taurine and indicine breed crosses, TT – taurine breed crosses, Breed groups and genotypes as given in Tables 1 and 2

Genotype	aB	aS	aZx	aZ	AC	mB	mS	mZx	mZ	mC	dD$_{II}$	dD$_{TI}$	dD$_{TT}$	mD$_{II}$	mD$_{TI}$	mD$_{TT}$
Purebred																
BB	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
SS	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
ZxZx	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
ZZ	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
F$_1$																
BS	0.5	0.5	0	0	0	1	0	0	0	0	0	0	1	0	0	0
SB	0.5	0.5	0	0	0	0	1	0	0	0	0	0	1	0	0	0
BZ	0.5	0	0	0.5	0	1	0	0	0	0	0	1	0	0	0	0
ZB	0.5	0	0	0.5	0	0	0	0	1	0	0	1	0	0	0	0
SZ	0	0.5	0	0.5	0	0	1	0	0	0	0	1	0	0	0	0
ZS	0	0.5	0	0.5	0	0	0	0	1	0	0	1	0	0	0	0
ZZx	0	0	0.5	0.5	0	0	0	0	1	0	1	0	0	0	0	0
ZxZ	0	0	0.5	0.5	0	0	0	1	0	0	1	0	0	0	0	0
ZxS	0	0.5	0.5	0	0	0	0	1	0	0	0	1	0	0	0	0
ZC	0	0	0	0.5	0.5	0	0	0	1	0	0	1	0	0	0	0
F$_1$ backcross																
(ZB)B	0.75	0	0	0.25	0	0.5	0	0	0.5	0	0	0.5	0	0	1	0
(ZB)Z	0.25	0	0	0.75	0	0.5	0	0	0.5	0	0	0.5	0	0	1	0
(ZS)S	0	0.75	0	0.25	0	0	0.5	0	0.5	0	0	0.5	0	0	1	0
(ZS)Z	0	0.25	0	0.75	0	0	0.5	0	0.5	0	0	0.5	0	0	1	0
(ZZx)Z	0	0	0.25	0.75	0	0	0	0.5	0.5	0	0.5	0	0	1	0	0
(ZxB)B	0.75	0	0.25	0	0	0.5	0	0.5	0	0	0	0.5	0	0	1	0
(ZC)Z	0	0	0	0.75	0.25	0	0	0	0.5	0.5	0	0.5	0	0	1	0
3-breed cross																
(BS)Z	0.25	0.25	0	0.5	0	0.5	0.5	0	0	0	0	1	0	0	0	1
(ZB)S	0.25	0.5	0	0.25	0	0.5	0	0	0.5	0	0	0.5	0.5	0	1	0
(ZZx)S	0	0.5	0.25	0.25	0	0	0	0.5	0.5	0	0	1	0	1	0	0
(ZC)S	0	0.5	0	0.25	0.25	0	0	0	0.5	0.5	0	0.5	0.5	0	1	0
Z(BS)	0.25	0.25	0	0.5	0	0	0	0	1	0	0	1	0	0	0	0
S(ZC)	0	0.5	0	0.25	0.25	0	1	0	0	0	0	0.5	0.5	0	0	0
F$_1$ x F$_1$																
(ZB)(SZ)	0.25	0.25	0	0.5	0	0.5	0	0	0.5	0	0	0.5	0.25	0	1	0
(ZS)(SZ)	0	0.5	0	0.5	0	0	0.5	0	0.5	0	0	0.5	0	0	1	0
(ZS)(ZC)	0	0.25	0	0.5	0.25	0	0.5	0	0.5	0	0	0.5	0.25	0	1	0
(BS)(ZC)	0.25	0.25	0	0.25	0.25	0.5	0.5	0	0	0	0	0.5	0.5	0	0	1

Table 5. Direct and maternal additive and dominance effects for various growth traits

Abbreviations as given in Table 4

	Birth weight (kg)	Weaning weight (kg)	Preweaning ADG (g/day)	Yearling Weight (kg)	Final Weight (kg)	Postweaning ADG (g/day)
aS	2.0±0.7**	16.4±3.0**	72.7±14.3**	24.5±3.7**	36.5±4.6**	59.8±9.6**
aZx	1.7±1.1	7.8±5.2	28.6±24.9	13.4±6.5*	27.9±8.1**	63.8±16.9**
aZ	4.0±0.6**	16.0±2.8**	63.4±13.1**	24.0±3.4**	42.1±4.2**	82.6±8.8**
aC	7.3±1.1**	46.4±4.9**	194.6±23.4**	49.7±6.1**	78.5±7.5**	97.2±15.6**
mS	1.4±0.6*	9.9±2.7**	46.7±12.9**	6.5±3.4	6.8±4.1	-6.5±8.7
mZx	-3.1±0.8**	14.7±3.8**	95.8±18.3**	10.2±4.8*	8.5±5.9	-19.1±12.3
mZ	-5.8±0.5**	13.3±2.4**	97.8±11.5**	10.2±3.0**	10.7±3.7**	-6.5±7.7
mC	1.5±1.3	4.3±6.0	16.4±28.6	7.8±7.4	3.9±9.1	-3.3±19.0
dD_{II}	1.5±0.5**	5.8±2.2**	24.0±10.6*	8.6±2.8**	11.0±3.4**	14.5±7.1*
dD_{TI}	1.7±0.3**	11.4±1.2**	49.7±5.6**	17.9±1.5**	26.2±1.8**	44.8±3.8**
dD_{TT}	0.2±0.5	6.2±2.3**	28.0±11.2*	5.7±2.9	7.1±3.6	4.9±7.5
mD_{II}	0.9±0.7	1.4±3.2	-1.7±15.0	8.7±4.0*	6.4±4.9	20.4±10.3*
mD_{TI}	1.1±0.3**	15.7±1.3**	73.1±6.0**	9.9±1.6**	7.1±1.9**	-25.8±4.0**
mD_{TT}	-1.5±0.8	5.8±3.4	36.3±16.2*	8.4±4.2*	4.5±5.2	-1.2±10.8

*P<0.05, **P<0.01

Table 6. Predicted means of F_1 genotypes based on the additive and dominance genetic effects shown in Table 5 along with correlation coefficient estimates between predicted and least squares means of these genotypes

Breed groups and genotypes as given in Table 1 and 2

Genotype	Birth Weight (kg)	Weaning Weight (kg)	Preweaning ADG (g/day)	Yearling Weight (kg)	Final Weight (kg)	Postweaning ADG (g/day)
BS	33.1	171	713	200	288	354
SB	34.5	181	760	207	295	347
BZ	35.6	176	730	212	310	405
ZB	29.8	190	828	222	321	399
SZ	38.0	195	814	231	335	429
ZS	30.8	198	865	234	339	429
ZZx	30.5	188	817	220	320	400
ZxZ	33.2	189	815	220	318	388
ZxS	32.4	195	845	229	330	407
ZC	33.5	213	926	247	360	447
Correlation	0.95	0.99	0.99	0.94	0.96	0.92

Table 7. Percentage heterosis (%) in selected F_1 genotypes (those where reciprocal crosses were available) for various growth traits

Genotypes as given in Table2

Genotype	Birth weight	Weaning Weight	Preweaning ADG	Yearling weight	Final weight	Postweaning ADG
SB / BS	2.1	2.2	1.5	3.8	1.3	1.7
ZB / BZ	8.2**	8.5**	8.0**	13.1**	12.7**	18.8**
ZS / SZ	4.0	5.4*	5.7*	7.0**	7.2**	9.2**
ZZx / ZxZ	4.2	2.5	2.2	2.8	2.6	2.5

*P<0.05, **P<0.01

Table 8. Comparison of some of the direct and maternal genetic effects reported in the literature with the present results.

Abbreviations as given in Table 4

	Present study[A]	Roberson *et al.*[B] (1986)	Arthur *et al.* [B] (1999)	Arthur *et al.* [B] (1999)
Environment	Tropical with low parasite challenge	Subtropical, USA	Subtropical, Australia	Temperate, Australia
Birth weight (kg)				
aZ	4.0**	4.6**	7.8**	1.7
mZ	-5.8**	-7.5**	-10.6**	-6.0**
dD_{TI}	1.7**	2.2**	9.1**	3.1
mD_{TI}	1.1**	0.6**	0.3	-0.7
Weaning weight (kg)				
aZ	16.0**	-12.9**	11.2	-22.9**
mZ	13.3**	13.1**	-8.2	3.4
dD_{TI}	11.4**	21.6**	53.5**	28.0**
mD_{TI}	15.7**	19.8**	72.6**	22.5
Preweaning ADG[C] (g/day)				
aZ	63.4**	-17.7**	14.0	-103.0**
mZ	97.8**	20.0**	10.0	39.0
dD_{TI}	49.7**	19.6**	185.0**	104.0**
mD_{TI}	73.1**	19.5**	301.0**	97

[A] Parameters expressed as Zebu deviation from BB mean (see Table 2).

[B] Parameters expressed as Brahman deviation from Hereford mean in respective climates.

[C] Preweaning gain given as kg difference between weaning weight and birth weight in Roberson *et al.* (1986).

**P<0.01

4.2 Appendix 2.

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Evaluation of beef cattle genotypes and estimation of direct and maternal genetic effects in a tropical environment

2. Adaptive and temperament traits

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Abstract

Data from a crossbreeding experiment conducted during 1992 – 1997 involving 31 genotypes from tropically adapted British (B), Sanga derived (S), Zebu cross (Zx), Zebu (Z), and Continental (C) beef cattle breed groups on adaptive traits such as mean tick counts (TICK), mean worm egg counts (EPG), mean rectal temperatures (TEMP) and mean coat scores (COAT), and temperament trait, mean flight time (FT) were analysed. The genotypes were grouped as *Bos taurus* (B, S, C) and *Bos indicus* (Z, Zx) derived to enable the comparison of direct (dD) and maternal (mD) dominance effects among indicine (II), taurine x indicine (TI) and taurine (TT) crosses. British breed group in this study consisted of Belmont Adaptaur, which is a tropically adapted selected line for tick resistance and 550-day liveweight and hence does not represent temperate British breeds. Coefficients of variation ranged between 15.1 and 55.4% and repeatability estimates varied between 0.26 and 0.45 in various adaptive and temperament traits. Significant ($P<0.01$) genotype differences with better performance of Zebu and its crosses over taurine crosses were noticed in all the adaptive traits. Although genotype differences were significant for FT, no clear trend was noticed. Direct additive components of Z and Zx expressed as a deviation from the British mean were significant and negative (favourable) for all the adaptive traits, except for EPG in Zx, indicating better adaptability of Zebu and its crosses relative to the British. Unfavourable additive effect for EPG in Sanga derived breed group and undesirable additive effect for TICK and COAT in Continental breeds relative to the British was observed. All the adaptive traits benefited by crossing as evidenced by significant and favourable dD effects in TI and TT crosses. Heterosis estimates were significant and favourable for all the adaptive traits in Z and B crosses. Treatment to control ticks and worms resulted in significantly increased live weight gains (LWG) in a majority of genotypes highlighting the negative impact of parasite burdens. As the *Bos indicus* proportion in the genotypes increased, the responses from treatment reduced. The additive effect of Z in the treated group was only half that of the control group, relative to the British breed mean, indicating the advantage of Zebus in the presence of parasites. Low and insignificant phenotypic correlations among TICK, EPG and LWG were observed. A significant positive correlation between TEMP and COAT and a negative correlation between TEMP and LWG was observed in the British purebreds.

Additional keywords: tick counts, worm egg counts, rectal temperatures, coat score, temperament, live weight gain, repeatability, heterosis, phenotypic correlation

Introduction

Growth in beef cattle in a tropical environment is influenced by their genetic potential for growth and their adaptation to environmental stressors like ticks, worms, high temperature, and humidity. In the extensive pastoral regions of Australia, the use of breeds that have inherently high parasite resistance makes sound economic sense, particularly because parasite control using chemicals is not feasible in most of these areas. Parasites acquiring resistance to the chemicals used to treat them compound these problems. The increasing awareness of chemical residues in meat and milk further necessitates the need to look for alternate strategies to control external and internal parasites. One of the most economic and easy solutions is to farm cattle that are resistant to the parasites. Hence, the present study aims to compare the tick and worm egg counts of various genotypes derived from a crossbreeding experiment as a measure of their tick and worm resistance.

The expression of a low rectal temperature in a hot environment is a good index of heat tolerance (Turner 1984). Genetic differences affecting heat tolerance are related to thermoregulatory attributes like an animal's coat type. Hence, the present study also aims to compare these genotypes for their rectal temperatures and coat scores. Temperament, as measured by the animal's flight time, is important in determining the ease of handling during mustering and so the present study also aims to determine the genotype differences in temperament.

Some early studies compared breeds for their resistance to ticks and worms (Turner and Short 1972; Utech *et al.* 1978; Frisch 1987), heat resistance (Turner 1982), coat score (Turner 1962), and temperament (Burrow and Corbet 2000). But there are very few studies examining a wide range of beef breeds for their resistance to parasites and heat and also temperament. An understanding of these adaptive and temperament traits and the effect of their control on live weight gain is essential in planning any crossbreeding program for tropical environments. This knowledge is even more important in optimising different breed combinations in a composite to suit the tropics or subtropics. Hence, an additional objective of this study is to estimate direct and maternal genetic effects for these adaptive and temperament traits. The effect of treatment to control ticks and worms on live weight gains and the phenotypic correlations among adaptive, temperament, and weight gain traits are also investigated.

Materials and methods

This crossbreeding study was conducted during 1992 – 1997 at the National Cattle Breeding Station, 'Belmont', near Rockhampton, Queensland, Australia. The station is located 25 km north of the tropic of Capricorn, 40 km from the coast. The climate is dry tropical with unreliable wet seasons, with two-thirds of rainfall occurring between December and March. Winter (June to August) is the “dry” period of low nutrition. Cattle are subjected to numerous environmental stressors like high temperatures and humidity during summer, nutritional deficiency during the “dry” season, ecto-parasites (*Boophilus microplus* and buffalo fly, *Haematobia irritans exigua*), endo-parasites (gastro-intestinal helminths or worms, predominantly *Haemonchus*, *Cooperia* and *Oesophagostomum* species), and periodic exposure to diseases (Bovine Infectious Kerato-conjunctivitis and Ephemeral fever). A more complete description of the background to this study is presented by Frisch and O’Neill (1998*a*, 1998*b*).

Breed pooling

Various breeds of African, European and Indian origin were crossed to compare a range of genotypes and to identify the most productive genotypes. Breeds were regrouped based on their origins and similarities (Table 1) producing 31 genotypes for evaluation. In this paper, B, S, Zx, Z, and C represent tropically adapted British, Sanga derived, Zebu cross, Zebu, and Continental breed groups respectively (Table 1). British purebred group in this study consisted of Belmont Adaptaur (Table 1), which is a tropically adapted selected line for tick resistance and 550-day liveweight. Hence its resistance levels in the tropical environment are expected to be higher than the non-adapted British breeds such as purebred Hereford, Shorthorn, and Angus. In crosses, the female parent is shown first with crossbred dams and sires shown in parentheses. Purebred performance information was not available for Boran, Tuli, Shorthorn, Charolais, and Simmental and they were only represented as crosses. A more complete description of the breed pooling was given in the previous publication (Prayaga 2003).

Data

Steers and heifers were managed as separate cohorts after weaning at around 6 months of age and calves from each crop were allocated randomly within sex, genotype, sire and previous lactation status of the dam into either a treatment group or a control group. Animals in the treatment group were treated regularly every 3 weeks from around 8 months of age to around 18 months of age with anthelmintic (Nilverm injection, Pitman – Moore, Australia) to control gastrointestinal nematodes. They were also inspected for cattle ticks (*Boophilus microplus*) and if ticks were present, all the treatment group animals were dipped in a plunge dip containing acaricide (Tactic, Hoechst, Australia). A more detailed description of the treatments and management is given by Frisch and O'Neill (1998*b*), and Prayaga (2003).

The abbreviations and definitions of the traits recorded for this study are shown in Table 2. TICK and EPG were recorded on all weaned animals over a nine-week period at three weekly intervals before commencement of the treatment. After this period, from around 8 months of age, TICK and EPG were recorded on control animals at various postweaning ages until 18 months of age. Within each cohort (year – sex subclass), all animals had the same number of records for each of the adaptive and temperament traits, although the number of records of each of the trait varied across cohorts (Table2). Data editing of TICK was based on the mean tick counts and the number of zero counts in each of the year – count number sub classes. If the number of zeros in any of these sub-classes was more than 25% and mean tick count was <10, the data from that particular sub-class was omitted from analyses because it was deemed that insufficient challenge existed to determine an animal's resistance to ticks.

In the COAT scoring system, each score was split into fractional scores to account for subclasses (for example, score 1 was again sub divided into 1-, 1, 1+ and 2 into 2-, 2, 2+ etc.,). For recording convenience, these fractional scores were converted as continuous numbers from 1 to 21 with 1-, 1, 1+ representing 1, 2, 3 and 2-, 2, 2+ representing 4, 5, 6 and so on. All analyses were conducted on converted scores (1 to 21) as it increased the sensitivity of scores. Mean coat scores were calculated over all available coat scores for each animal, which were spread over the 10-month recording period across seasons. Initial analyses of data showed that coat scores followed the same pattern of sleek coats in summer and woolly coats in winter months across all breed groups.

For flight time measurements, records that were >2.85s were included in the analyses by equating their flight time (FT) as 2.85s, as they represented highly docile animals. These higher time recordings are because the animal did not move from the crush after activating the recorder beam. Data editing of weight traits for calculating LWG was discussed by Prayaga (2003).

Statistical analysis

Data on TICK, EPG, TEMP, COAT, and FT were analysed using a univariate fixed effects model (model 1) in ASREML (Gilmour *et al.* 2001). Model 1 included the effects of genotype, contemporary group (consisting of year of birth, season of birth and age of dam), sex, and previous lactation status of the dam. Treatment was also included as a fixed effect in the analysis of TEMP and FT data. Treatment was not significant for COAT and hence not included. Year of birth ranged from 1991 to 1996 and months of birth were regrouped into 3 seasons (August – September, October – November and December – January). Age of dam at the time of calving was grouped into 3, 4, 5, and ≥ 6 years. Previous lactation status of the dam was categorised as wet cow, dry cow, cow with a dead calf and maiden heifer. After testing the possible first order interactions for significance, the significant interaction effects were included in the analysis. Data pertaining to TICK and TEMP were subjected to $\log_{10}$ transformation and EPG was subjected to cube root transformation. Analyses were conducted both on transformed and non-transformed data. As the transformation did not affect the significance tests, only least squares means from non-transformed data are presented in this paper. For FT, the first two postweaning measures were also separately analysed to test whether repeated handling of animals had influenced the genotype differences in temperaments. As the results from the analysis of the first two measures and the overall mean postweaning measures were similar, only the latter are presented.

For the estimation of repeatability, data on repeated measures of each of the adaptive and temperament traits were used. Transformed data were used for this repeated measures analyses wherever applicable. The number of records, number of animals, and the average number of records per animal included in these analyses are presented in Table 3. The model (model 2) included the above-mentioned effects from model 1, and a random effect of animal. In this model, record number was also included as a fixed effect to correct for the differences in the postweaning ages at which these repeated measures of each trait were recorded. In the analyses of TEMP, crush number within each recording was included in the model to account for the differences in time and hence ambient temperatures, before recording rectal temperatures.

For the estimation of direct and maternal additive, and direct and maternal dominance effects, the fractional coefficients of genetic effects (Prayaga 2003) of various genotypes were used. Because of the linear dependencies due to Σa_i (direct additive coefficients) =1 and Σm_i (maternal additive coefficients) =1, the full set of direct and maternal additive effects could not be estimated. Hence, the British breed group direct and maternal additive coefficients (aB, mB) were not included in the model and genetic components of other breed groups were estimated as a deviation from the British breed group (BB) mean. For the estimation of direct and maternal dominance effects, genotypes were regrouped into *Bos indicus* x *Bos indicus* (II), *Bos taurus* x *Bos indicus* (TI) and *Bos taurus* x *Bos taurus* (TT) crosses. For the purpose of this regrouping B, S, and C were regarded as *Bos taurus* derived breeds and Z and Zx were regarded as *Bos indicus* derived breeds. Hence, the direct dominance (dD) effects for various genotypes were grouped as dD_{II}, dD_{TI} and dD_{TT} and maternal dominance (mD) effects for various genotypes were grouped as mD_{II}, mD_{TI} and mD_{TT}. This was necessary because of lack of information on all the reciprocals. The genetic effects were estimated as partial regression coefficients by treating the fractional coefficients as continuous variables in the analysis using the following model (model 3) with ASREML (Gilmour *et al.* 2001):

$$Y_{ij} = \mu + F + b_1 A + b_2 M + b_3 dD + b_4 mD + e_{ij}$$

Where, Y_{ij} is j^{th} observation on the i^{th} animal; μ is least squares mean of British breed group (BB); F are all the significant effects included in model 1; b_1 are partial regression coefficients representing direct additive effects of S, Zx, Z, and C expressed as a deviation from BB mean; b_2 are partial regression coefficients representing maternal additive effects of S, Zx, Z, and C expressed as a deviation from BB mean; b_3 are partial regression coefficients representing direct dominance effects of II, TI and TT crosses; b_4 are partial regression coefficients representing maternal dominance effects of II, TI, and TT crosses; A and M represent the fractional coefficients of direct and maternal additive effects for S, Zx, Z and C breed groups and dD and mD represent the fractional coefficients of direct and maternal dominance effects for II, TI and TT crosses.

Heterosis was estimated using least squares means for each trait as a deviation of the F_1 mean from the parental population mean and expressed as a percentage of the parental population mean. Heterosis estimates were only derived for those F_1 crosses where reciprocals existed.

To study the effect of treatment to control ticks and worms on weight gain, LWG data were analysed using a univariate fixed effects model (model 4) using ASREML (Gilmour *et al.* 2001). Model 4 included effects of genotype, contemporary group, sex, treatment, and previous lactation status of the dam. Age at final weighing was included as a covariate to adjust for the age differences. Significant first order interactions were also included in the model. Least squares means of the treated and control animals within each genotype were derived from this analysis. Response to treatment was calculated as the difference between treated and control group means within each genotype. To compare crossbreeding parameters of treated and control animals for LWG, data were analysed separately using a genetic effects model (model 5), with the fixed effects and covariates similar to model 4 and the fractional coefficients of genetic effects as covariates (similar to model 3).

Phenotypic correlations among various adaptive and temperament traits and LWG were estimated within the two extreme genotypes i.e. ZZ and BB with 277 and 301 animals respectively, using a multivariate analyses by including all the significant fixed effects for various traits with ASREML (Gilmour *et al.* 2001). ZZ and BB were selected for comparing phenotypic correlations, as they were distinctly different in their levels of adaptation.

Results

Coefficient of variation and repeatability

Average number of records per animal included in the analyses ranged between 2.13 (TICK) and 6.21 (FT). Tick counts, worm egg counts, and flight time were found to be highly variable with CV values ranging between 37.0 and 55.4 % and rectal temperatures and coat scores were moderately variable with CV values of 18.9 and 15.1%, respectively (Table 3). Moderate to high repeatability values ranging between 0.26 and 0.45 for the adaptive and temperament traits were observed.

Genotype differences

Analysis of variance showed that all the adaptive and temperament traits were significantly ($P<0.01$) affected by genotype, contemporary group and sex, and TEMP and FT were significantly ($P<0.01$) affected by treatment. Previous lactation status of the dam was not significant ($P>0.05$) for any of these traits. The genotype x sex interaction was significant for TICK ($P<0.05$), EPG, and TEMP ($P<0.01$). A sex x treatment interaction was significant ($P<0.05$) for TEMP. Least squares means for various adaptive and temperament traits along with their genotype rankings within the trait are presented in Table 4. These genotype rankings are only indicative of the respective position of the genotype within the trait of interest and are not based on significant differences. Although the least significant difference based on the overall standard error of difference was computed for any pair wise comparisons (Table 4), it should be noted that only pre-planned comparisons (with respective standard errors of difference) could be made with sufficient accuracy because of the large number of means derived simultaneously.

Despite the low to moderate tick and worm challenges, genotype differences in tick and worm egg counts were significant. The overall mean TICK during the period of study was 18 ticks / animal, with (ZC)S having the highest TICK of 34.7 followed by BB with 29.1. The lowest TICK was observed in ZxZ (9.5) followed by (BS)Z (9.9), and ZZ (10.3). Among purebreds, there was a clear distinction between BB and SS with high tick counts and ZxZx and ZZ with low tick counts. In crossbreds, as the Zebu proportion in the cross increased, TICK decreased. Within F_1s, except in ZC, crosses with 50% Zebu proportion showed lower TICK. In F_1 backcrosses, lower tick counts were observed in (ZB)Z, (ZS)Z, and (ZZx)Z where Zebu proportion was ≥ 75%. Low to moderate tick counts were observed in 3-breed crosses and F_1 x F_1 crosses except in (ZC)S.

The overall mean EPG was 458 eggs/g faeces and varied between 274 ((ZB)Z) and 781 (SS) eggs/g. Among purebreds, ZZ and SS recorded significantly ($P<0.05$) lower and higher EPG respectively. Among F_1s, ZB had the lowest EPG and BS (100% *Bos taurus*) had the highest EPG. The effect of higher proportion of Zebu on reducing EPG was evident in F_1 backcrosses with (ZB)Z, (ZS)Z, and (ZZx)Z (with ≥ 75% Zebu contribution) having lower mean EPG. All the 3 breed crosses with lower Zebu proportions had high mean EPG.

The overall mean TEMP was 39.47^0C and varied between 39.35^0C in (ZS)Z and 39.85^0C in BB. Among purebreds, British breeds (BB) were susceptible to high ambient temperatures, with significantly ($P<0.05$) higher rectal temperatures. The Zebu breed group had significantly ($P<0.05$) lower rectal temperatures (39.38^0C) demonstrating their resistance to heat stress. Among F_1s, ZxS, ZB, ZS, and ZZx (with ≥ 50% *Bos indicus*) had lower TEMP. In F_1 backcrosses, crosses with ≥ 75% of Zebu genetic contribution had lower TEMP. In 3 breed crosses and F_1 x F_1 crosses, TEMP was generally lower than or equal to the overall mean.

The overall mean COAT was 8.50 and varied between 7.20 (ZZ) and 12.05 (BB). This variation ranged from 3- to 4+ in the original scores, meaning coats were fairly short (generally smooth coated) in Zebus and fairly long (with the coat turning rough and with patches of hair being curved outwards) in the British breeds. Among F_1s, ZS, ZxZ, and SZ had desirable lower COAT whereas SB, BS, and ZC had relatively higher COAT. Backcrosses with ≥ 75% Zebu contribution had sleek coats. Crosses with ≥

75% British contribution (e.g. (ZB)B and (ZxB)B) had higher COAT indicating hairy and woolly coats.

The overall mean FT was 1.37s, varying from 1.16s in (BS)Z to 1.57s in (ZxB)B. All purebred genotypes had almost identical FT with no significant differences among them. Among F_1s, BS had the lowest FT (1.17s) and ZZx the highest FT (1.54s). Among backcrosses, except in (ZxB)B, FT was similar to the overall mean. In 3 breed crosses, (BS)Z and Z(BS) had low FT.

Genetic effects

Crossbreeding parameters or the direct and maternal genetic effects estimated for the adaptive and temperament traits are presented in Table 5. For all adaptive traits, the direct additive component of Zebu (aZ) was significantly negative relative to the British breed mean (BB) suggesting better adaptation of Zebus. The aZx was significantly negative (favourable) relative to BB mean for TICK, TEMP, and COAT, but at a lower magnitude than aZ. The aS was significant and positive relative to BB mean for EPG indicating an undesirable additive effect of worm egg counts in Sanga derived group relative to the British breed group. However, a significantly ($P<0.01$) negative aS for TEMP and COAT demonstrated a favourable effect of Sanga derived group relative to BB in these traits. The aC was significant and positive for TICK and COAT suggesting an undesirable additive effect of Continental breeds relative to BB.

Among maternal additive components, Zebu showed significantly negative (favourable) estimates (mZ) for EPG, TEMP and COAT. The mC showed a significant but undesirable positive effect for EPG. Though mS and mZx showed desirable negative effects in all the adaptive traits, they were only significant for COAT. *Bos taurus* x *Bos indicus* and *Bos taurus* x *Bos taurus* crosses benefited from heterosis as evidenced by significant negative dD_{TI} and dD_{TT} effects for all the adaptive traits except for the dD_{TT} component in EPG. Crossbred (*Bos taurus* x *Bos indicus*) dams contributed significant and desirable negative maternal dominance effects (mD_{TI}) for EPG, TEMP and COAT traits.

Both aS and aZ were significantly negative for FT relative to British breeds, suggesting that Zebu and Sanga derived breeds had poor temperament. However, because of their positive maternal additive effects (mS and mZ) of similar magnitude, the purebred SS and ZZ were similar to British breeds in temperament. None of the other additive effects were significant. dD_{TI} and dD_{TT} for FT were significant and negative indicating that crossbreeding resulted in animals with poorer temperaments.

Heterosis

Heterosis percentages in selected F_1 genotypes ranged from –40 to 7% for TICK, -20 to –9% for EPG, -0.32 to 0.04% for TEMP, -11.6 to –1.1% for COAT and –6.6 to 0.3% for FT (Table 6). Negative heterosis was desirable for the adaptive traits and positive heterosis was desirable for temperament (FT). Heterosis estimates were significant and negative (desirable) for all adaptive traits in Z and B crosses. In another *Bos taurus* x *Bos indicus* cross under study (i.e. Z and S crosses) heterosis was only significant for EPG and COAT. In crosses of S and B breed groups, significant and negative heterosis percentages of –35% and –9.1% were estimated for TICK and COAT. For FT, heterosis percentages were significant and negative (unfavourable) for Z and B crosses, and S and B crosses.

Effect of treatment on live weight gain

The overall LWG between 8 and 18 months was 129 kg in treated animals and 113 kg in control animals with a significant response of 16 kg overall genotypes (Table 7). Among all genotypes, SB (100% *Bos taurus*) benefited most (31 kg) by treatment and ZZx (predominantly *Bos indicus)* benefited the least (0 kg). Among purebreds, SS genotype showed high response (26 kg) to treatment. ZZ only benefited from treatment by 10 kg. As the *Bos indicus* proportion in the genotype increased, the benefit from treatment reduced as evidenced by insignificant and low responses. Among crossbreds, ZZx, ZxZ and (ZZx)Z had low or insignificant responses to treatment suggesting no benefit from treatment in Zebu crosses when tick and worm challenges were in the low to moderate range. However, significant responses in LWG from treatment among the majority of genotypes in the present study stressed the negative impact of parasite burdens on weight gain.

Another way to examine the differential responses to treatment is to compare their genetic effects (Table 8). Relative to the British breed mean, aZ of treated animals was only half that of the control group. The aZx, as a deviation from the British mean, was significant in the control group but not in the treated group. The aS and the aC were approximately the same in both treated and control groups. The dD_{TI} and the mD_{TI} had a significant positive and negative effect respectively in both treated and control groups. The magnitude of the dD_{TI} effect was lower in the treated group compared to the control group. In controls, dD_{II} also had a significant positive effect, which was not significant in treated animals.

Phenotypic correlations

Phenotypic correlations between TICK and EPG and their relationship with LWG were generally low and insignificant in both ZZ and BB breed groups (Table 9). TEMP and COAT were significantly ($P<0.01$) positively correlated (0.39) in BB, but the correlation was low and insignificant in ZZ. TEMP and COAT were negatively correlated with LWG in both ZZ and BB breed groups, however, the magnitude of relationship was higher in BB than ZZ. TEMP and COAT were significantly ($P<0.05$) positively correlated with TICK in BB indicating that animals carrying fewer ticks may also have lower TEMP and COAT scores. FT had significant (P<0.01) negative relationships with TEMP in both breed groups, suggesting that animals with lower rectal temperatures tend to have high flight times i.e. better temperaments.

Discussion

Coefficient of variation and repeatability

The moderate to high CV values observed for the adaptive and temperament traits in this study indicate high variation and hence good scope for selection. Burrow (2001) reported coefficients of variation of 48.03, 27.17, 19.5, and 38.3% for TICK, EPG, TEMP, and FT, respectively, which are comparable to the present estimates of 55.4, 37.0, 18.9, and 40.1%. The slightly higher variation in TICK and EPG in the present study could be due to the inclusion of estimates from 31 different genotypes whereas the earlier study represented only two breed groups.

The moderate to high repeatability estimates observed in the present study indicate that multiple measurements may not add greatly to the accuracy of these traits and there is relatively high correlation between repeated measures of the same individual. Hence, two to three postweaning measurements of any of these traits will accurately indicate the average performance for the trait of interest. The repeatability of TEMP (0.27) reported by Burrow (2001) is comparable to the present study but the repeatability of TICK (0.49) and EPG (0.28) differ from the present estimates. This may be due to the lower mean tick counts and higher mean worm egg counts in the present study compared to the earlier study. The repeatability of TEMP can be compared with some of the previous estimates in the range of 0.27 to 0.33 (Turner 1984). The repeatability of COAT in the present study (0.31) is lower than the estimate (0.6) reported by Turner and Schleger (1960). As the present estimates were based on repeated coat scores over different seasons throughout the year, the repeatability is expected to be lower than the estimates based on measures within each season, as the coat type is known to change across seasons. A higher repeatability (0.39) for FT is observed in the present study compared to 0.18 reported by Burrow (2001).

Genotype differences

Although there are significant genotype differences, even in the most resistant breeds and crosses at least 20% of animals can be categorised as lowly resistant or susceptible (Utech *et al.* 1978; Frisch 1999). Hence, to effectively breed for tick resistance in tropical environments, it is necessary to identify and cull the animals with low resistance and to select superior highly resistant males as parents of the next generation. Selection both within breeds and in resulting crosses is essential even in systematic crossbreeding programmes in maintaining high levels of tick resistance, as the resistance gained through crossbreeding can be lost in later generations if inappropriate crosses are used. The observed increase in tick resistance with the increase in Zebu proportion in the cross is comparable to the results reported by Seifert (1971) and Lemos *et al.* (1985). The significantly higher TICK and EPG in the British crosses relative to the Zebu crosses in this study is comparable to the differences reported by Turner and Short (1972).

Zebu crosses in the present study are more resistant to heat stress than the tropically adapted British cattle and therefore less prone to hyperthermia which is in agreement with Turner (1982). Although the range of TEMP in the present study is only 0.5^0C, because of the biological variation possible in this trait genotype differences were significant. The lower TEMP in 3-breed crosses in the present study, even those containing only 25% Zebu shows that heat tolerance can be improved by proper crossing and exploitation of heterosis.

Sleek coats in Zebu and its crosses compared to the British breeds was also reported by Turner and Schleger (1960). Coat type is a major determinant of temperature control and the similarities in the rankings of TEMP and COAT, at least in purebreds, shows the degree of interdependence between these traits. Olson *et al.* (2003) also reported that cattle with sleek hair maintained lower rectal temperatures than those of their normal coated contemporaries within the same breed composition. However, lower rectal temperatures can be explained by sleek hair only in part as low temperatures may also be due to a higher sweating rate or lower heat production (Turner and Schleger 1960). Within British breeds, coat type is reported to be closely related to heat tolerance and is of wider significance as an index of adaptation in tropical environments (Turner, 1962). This suggests that degree of relationship between TEMP and COAT differ between breed groups and is discussed further in later sections.

No clear trend in genotype rankings for FT is contradicting earlier reports of *Bos indicus* breeds being difficult to handle under extensive management conditions than the *Bos taurus* breeds (Burrow 1997). Burrow and Corbet (2000) reported lowest FT in the progeny of Limousin (Continental) sires crossed with Brahman dams indicating they had the least desirable temperaments. This contrasts with the present insignificant differences between Continental crosses and purebreds. They also opined that Continental breeds either have a specific negative combining ability when crossed with Brahmans, or themselves have temperaments that are no better than those of *Bos indicus*. In the present study all purebreds recorded similar FT indicating similar temperaments. In their study also, FT did not vary much among crosses between Brahman dams and some sire breeds, Angus (1.97), Belmont Red (1.93), Brahman (1.90) and Hereford (1.86) where *Bos indicus* proportion varied between 50 to 100%.

Genetic effects

Direct and maternal additive and dominance effects provide evidence of the direction and magnitude of breed contributions for the traits of interest. There are no other known reports in the literature on crossbreeding parameters for adaptive and temperament traits. However, these adaptive traits are of paramount importance in tropical environments. Hence, these parameters in combination with parameters for growth (Prayaga 2003) add considerable value to the process of making crucial breeding decisions in tropical environments. The positive and significant aC (+21.7 ticks) for TICK emphasises that Continental breeds are the least tick resistant breeds as also reported by Utech *et al*. (1978). Based on the direct additive effects, it is also evident that though the tick resistance of Sanga and British breeds is similar, there are significant differences between the breeds in their worm resistance levels. The similarity in the tick resistance levels of the British and the Sanga derived breeds in the present study may be due to the selection for tick resistance in tropically adapted British as explained earlier.

Worm resistance is influenced by both direct and maternal additive and dominance breed effects whereas tick resistance is influenced only by direct additive and dominance breed effects. The maternal influence of Zebu on worm resistance resulting in a significant decrease in faecal egg counts may be due to the transfer of maternal antibodies that promote resistance from mother to calf either via colostrum or perhaps in-utero transfer. The importance of Zebu as a maternal breed in this tropical environment is also emphasised by the significant and favourable mZ in all adaptive traits except TICK. Based on earlier results for growth traits (Prayaga 2003) and from the present parameters on adaptive traits, Zebu seems to be best suited as a maternal breed in a crossbreeding programme in the tropics. However, information on fertility traits will affect this observation, as Zebu breeds are known for their relatively low fertility rates (Frisch *et al.* 1987). But the loss in productivity through low fertility rates may be well compensated by the gains through high parasite and heat resistant attributes and relatively higher growth traits in tropical conditions. Low fertility in these maternal lines can also be addressed through the use of crossbred dams. As the direct additive effects of Z for TICK and EPG are significantly negative and dD_{TI} is also significantly negative, the ideal way to increase tick and worm resistance from a British breed base in the breeding population is to increase the Zebu proportion through crossbreeding. Although resistance of crossbreds to specific stressors is perceived to be directly related to the proportion of resistant breeds in the cross (Lemos *et al.* 1985), implying an additive nature of resistance traits, the significant dominance effects in the present study highlight the importance of crossing to also exploit nonadditive gene actions.

The similarity of additive and dominance effects of various breed groups for TEMP and COAT also substantiates their interdependence to a certain extent. Evidence of a major gene influencing hair coats and thereby heat tolerance in *Bos taurus* cattle from a study in USA (Olson *et al.* 2003) gives a better understanding of the mode of inheritance of hair coat and can be used in crossbreeding programmes to design hair coats according to the environment. The least heat resistance of the British and the Continental breeds as evidenced by the additive genetic effects agrees with the general perception of lower heat tolerance of taurine breeds. Significant and negative dD_{TI} and dD_{TT} for TEMP and COAT indicate that these traits can be effectively improved by exploiting hybrid vigour through crossbreeding. *Bos indicus* x *Bos indicus* crosses are unlikely to benefit because of the lack of differences between their parental breeds in resistance to heat. Taurine crosses (TT) may benefit because the parental breeds differ in their levels of adaptation to the tropical stressors. For example, the Belmont

Adaptaur (Hereford – Shorthorn cross) that comprises the BB population in this study was selected for tick resistance for several generations (see Frisch *et al.* 2000). Hence it may have developed genetically dissimilar configuration to the other taurine breeds in terms of its tropical adaptability, thereby allowing significant expression of dD_{TT} for TICK, TEMP and COAT when crossed to the Sanga derived breeds.

Heterosis

The significant heterosis effects are a consequence of the significant dominance effects discussed in the earlier section on genetic effects. The significant heterosis for COAT in most of the crosses where heterosis is estimated contrasts to that observed for TEMP, indicating some independence between the traits. Turner and Schleger (1960) also reported the influence of hybrid vigour on coat score, however, the magnitude of effect was not quantified in that study.

Effect of treatment on live weight gain

The response to treatment enables us to compare various genotypes for their potential to thrive in tick and worm infested areas. Based on these results, treatment to control ticks and worms does not improve the growth of Zebu animals to an economically viable extent. In British and Sanga breed crosses, treatment to control ticks and worms significantly affected LWG, but even in those instances, careful consideration would need to be given as to the economic viability of treating animals to the extent that occurred in this study.

Turner and Short (1972) reported a significant weight gain in Africander and British breed crosses, but not in Brahman crosses for anthelmintic treatment to control worms. They also reported non-significant gains in Africander and Brahman crosses, but a significant gain in British crosses for treatment against ticks by dipping once in every 3 weeks in a treatment period of 27 weeks. In their study, tick burdens were moderately high (27 – 93 ticks per side) and worm egg counts were low (112 – 144 eggs) relative to the present study. The higher magnitude of aZ and aZx in the control group compared to the treated group shows the importance of the direct additive contribution of Zebu under parasite challenge in a crossbreeding programme. This difference in additive effects also explains the observation by Frisch and O'Neill (1998*b*) that Brahmans show a slightly depressed growth rate when untreated, but significantly exceed the growth rate of British breeds. The relatively higher magnitude of dominance effects in II and TI crosses of control group compared to treated group emphasise that heterosis can be better realised in untreated animals. This is because under parasite challenge, the genetic distance between parental breeds increases due to the component of genetic differences relating to resistance to parasites that is otherwise not accounted for in treated animals.

Hence in a tropical environment where treatment may not be economically viable , various options to improve growth performance without investing on treatment to control parasites are: (i) Crossing indicine breeds when the parasite challenge is high as it exploits favourable direct and maternal additive effects of growth and adaptive traits and the dD_{II} effects for growth. (ii) Crossing taurine – indicine breeds where the parasite challenge is low to moderate and maintaining taurine purebreds is feasible, as it exploits desirable high dD_{TI} effects for growth and adaptive traits. Even in a high parasite challenge area this is a viable option if artificial breeding or tropically adapted taurine bulls can be used. (iii) Deriving and developing an optimal composite based on economic weights and crossbreeding parameters of growth and resistance traits (Prayaga *et al.* 2003).

Phenotypic correlations

Low and insignificant phenotypic relationships between traits related to parasite resistance (TICK and EPG) and LWG in both the BB and ZZ breed groups indicate that in an environment with low to moderate parasite infestation, tick and worm egg counts individually may not have a significant effect on growth in either susceptible (BB) or resistant (ZZ) breeds. This is unlikely to be the case in environments with more severe parasite challenge. Mackinnon *et al.* (1991) and Fordyce *et al.* (1996) also reported low phenotypic correlations between tick burdens and growth. This observation is made despite the evidence that tick and worm control through treatment improves the growth performance in various genotypes as reported in the present study and elsewhere in the literature (Holroyd *et al.* 1988). Hence, total removal of ticks and worms through treatment may have a significant beneficial effect on live weight gain but in the presence of these stressors, weight gain seems to be almost independent of the number of ticks and worms in a low to moderate challenge within each breed group. However, Frisch (1999) reported that the reduction in growth performance is directly proportional to the number of engorging ticks across a wide range of cattle genotypes. So very high levels of infestation may cause a noticeable impact on growth performance.

The negative (favourable) phenotypic correlation observed between TEMP and LWG suggest that as animals are better equipped to handle heat stress they gain weight at a faster rate. Burrow (2001) also reported a favourable (negative) phenotypic correlation between rectal temperature and growth traits in a tropically adapted composite line. However, the difference in the magnitude of this negative relationship between breed groups in the present study suggest that TEMP plays a more significant role in regulating live weight gains in British breeds than in Zebus. This observation substantiates the claim that Brahman and Brahman cross cattle regulate body temperature efficiently in that productivity is little reduced in hot environments (Turner 1984). Coat type is a major determinant of temperature control, through which it affects growth rate (Turner 1984), but there is some correlation between coat type and growth rate, independent of thermal effects (Turner, 1962). Similar to TEMP, COAT also showed differences in the magnitude of its relationship with LWG between two breed groups. Turner and Schleger (1960) also reported that the correlation between coat score and growth rate is high in British breeds though its relationship in Zebus is inconclusive. The low and positive correlation between COAT and TICK in BB suggests that animals with sleek coats have fewer ticks than the animals with woolly coats. Turner and Schleger (1960) explained this by stating that a short coat would facilitate removal of ticks by licking. The heat- susceptible British breeds showed greater interdependence between rectal temperatures and coat types than the heat resistant Zebu breeds. This substantiates the earlier observation that heat regulation in Zebu crosses may also be due to higher sweating rate and lower heat production.

The significant negative relationship between TEMP and FT (-0.24) reported by Burrow (2001) is comparable to the present observation of negative phenotypic correlation between TEMP and FT in both the breed groups. Lower rectal temperature may be due to the less or slower movement of better temperament animals causing lower heat load. Hence, these lower rectal temperatures may be a consequence of reduced activity of better temperament animals rather than the increased heat resistance.

Conclusions

The variation in adaptive and temperament traits would facilitate the implementation of selection programmes for their improvement. Crossbreeding results in progeny with better adaptation, relative to *Bos taurus* breeds, with resulting genotypes performing better even in tropical environments. Zebu and its crosses with taurine breeds have shown better adaptability than taurine crosses. The variability in direct additive and dominance effects of adaptive traits in various breed groups can be efficiently used for defining optimal crossbreeding systems. As the number of traits that need to be considered for assessing total genetic value of a cross increases, the importance of deriving an optimal composite relative to systematic crossbreeding also increases. The crossbreeding parameters for adaptive traits from this study in combination with the parameters for growth traits (Prayaga 2003) can be utilised to derive an optimal composite in low to moderate tick and worm infested tropical environments. A strategic selection programme implemented thereafter in such a composite is bound to derive favourable results. The importance of including tick, worm, and heat resistance data when designing any breeding programme for tropical environments is well highlighted by the significant differences between various genotypes in their resistance levels and the improvements in live weight gains of treated animals. Further studies on genetic correlations between adaptive and growth traits in various breed groups available for crossbreeding are essential to substantiate any conclusions drawn regarding responses to selection.

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Table 1. Breed group formation from the breeds involved in the study

Breed group name	Dam breeds	Sire / Sire of the dam breeds
Bos taurus derived		
Tropically adapted British (B)	Belmont Adaptaur (HS) (Synthetic breed of ½ Hereford, ½ Shorthorn)	HS Shorthorn*
Sanga derived (S)	Belmont Red (AX) (Synthetic breed of ½ Africander, ¼ Hereford, ¼ Shorthorn)	AX, Tuli (Tu)
Continental ©	-	Charolais (Ch), Simmental (Si)
Bos indicus derived		
Zebu (Z)	Brahman (Bh)	Brahman (Bh), Boran (Bo)
Zebu cross (Zx)	Belmont Brahman cross (BX) (Synthetic breed of ½ Brahman, ¼ Hereford, ¼ Shorthorn)	BX

*Only represented as the sire breed of crossbred dams

Table 2. Abbreviation and definition of the traits recorded

Trait	Definition
	Adaptive traits
TICK	Mean number of ticks recorded at various postweaning ages by counting the number of engorging ticks of ≥ 4.5 mm long on one side of the animal following field infestations (Wharton *et al.* 1970)
EPG	Mean number of worm eggs per gram of faeces at various postweaning ages (Roberts and O'Sullivan 1950) as recorded by one experienced technician
TEMP	Mean rectal temperatures of animals recorded at various postweaning ages during summer months when the ambient temperatures were > 30^0C
COAT	Mean coat scores of animals averaged over various postweaning scores. The scoring system was subjective and ranged between 1 (extremely short and sleek coat) to 7 (very woolly coat) as described by Turner and Schleger (1960)
	Temperament
FT	Mean flight time of animals, the electronically recorded time taken (in hundredths of a second) for an animal to cover a fixed distance (1.7 m) after leaving the weighing crush (Burrow *et al.* 1988) at various postweaning ages. Low flight times indicate poor temperaments and high flight times indicate desirable docile temperaments
	Growth traits
LWG	Liveweight gain (kg) estimated as a deviation of 8 month weight from 18 month weight in animals under study. Weights were recorded at various postweaning ages as described in the previous paper (Prayaga 2003)

Table 3. Coefficent of variation and repeatability estimates for adaptive and temperament traits under study

	Tick count	Worm egg count	Rectal temperature (^oC)	Coat score	Flight time (s)
No. of records	4993	7229	8119	10841	15877
No. of animals	2346	2591	2540	2576	2555
No. of records per animal (range)	1-4	1-6	1-5	1-6	1-9
Av. no. of records per animal	2.13	2.80	3.20	4.21	6.21
Phenotypic variance	0.21±0.01	5.96±0.12	0.005±0.0001	1.62±0.03	0.30±0.005
Coefficient of variation (%)	55.4	37.0	18.9	15.1	40.1
Repeatability	0.26±0.02	0.45±0.01	0.31±0.01	0.31±0.01	0.39±0.01

Table 4. Least squares means and standard errors of adaptive and temperament traits of various genotypes under study with rankings of genotypes given in parentheses

Differences between means >9.3 ticks, >168 worm eggs, >0.14^{o}C, >0.38 and 0.15s (based on overall standard error of difference) are significantly different ($P<0.05$) for tick counts, worm egg counts, rectal temperature, coat scores and flight times respectively; Traits as defined in Table 2; N – number of records; Breed group in genotype as given in Table 1 with female breed given first in the crosses and crossbred dams and sires identified in parentheses

Genotype	N	TICK	N	EPG	N	TEMP (^{o}C)	N	COAT	N	FT (s)
Overall	2346	18.0±1.1	2591	458±20	2540	39.47±0.02	2576	8.50±0.05	2555	1.37±0.02
Purebreds										
BB	261	29.1±1.6(30)	310	622±30(28)	289	39.85±0.03(31)	300	12.05±0.07(31)	297	1.42±0.03(22)
SS	209	27.9±1.7(29)	226	781±32(31)	224	39.53±0.03(24)	227	8.78±0.07(22)	223	1.41±0.03(20)
ZxZx	56	12.3±3.1(6)	56	498±59(20)	55	39.50±0.03(21)	56	8.73±0.14(21)	55	1.44±0.05(26)
ZZ	250	10.3±1.6(3)	277	319±29(5)	269	39.38±0.03(4)	280	7.20±0.07(1)	273	1.44±0.03(25)
F_1										
BS	46	19.3±3.4(19)	46	710±66(30)	46	39.53±0.06(25)	46	9.26±0.15(27)	46	1.17±0.06(2)
SB	22	18.0±5.4(18)	23	554±98(26)	22	39.64±0.08(30)	23	9.67±0.22(29)	23	1.49±0.08(29)
BZ	93	10.3±2.5(4)	94	458±47(16)	95	39.56±0.04(27)	94	8.68±0.11(20)	94	1.26±0.04(5)
ZB	98	13.2±2.4(11)	115	291±42(2)	112	39.42±0.04(11)	113	8.34±0.10(16)	113	1.41±0.04(21)
SZ	139	13.0±2.1(9)	139	492±40(19)	135	39.48±0.03(19)	136	7.78±0.09(7)	135	1.30±0.04(8)
ZS	157	16.0±2.0(14)	178	431±35(14)	177	39.42±0.03(10)	177	7.65±0.08(3)	176	1.39±0.03(17)
ZZx	51	14.6±3.3(12)	52	326±63(7)	52	39.41±0.05(9)	52	8.05±0.14(13)	51	1.54±0.05(30)
ZxZ	103	9.5±2.4(1)	103	416±45(13)	103	39.50±0.04(22)	103	7.70±0.10(6)	103	1.35±0.04(12)
ZxS	52	17.1±3.2(16)	55	570±60(27)	53	39.40±0.05(8)	56	8.46±0.13(19)	56	1.40±0.05(18)
ZC	79	26.3±2.6(28)	91	320±47(6)	90	39.50±0.04(23)	91	9.26±0.11(26)	91	1.43±0.04(23)
F_1 backcross										
(ZB)B	56	22.5±3.2(24)	56	402±60(12)	56	39.59±0.05(28)	56	9.35±0.14(28)	56	1.32±0.05(10)
(ZB)Z	108	13.1±2.4(10)	121	274±43(1)	120	39.40±0.04(7)	121	7.70±0.10(5)	120	1.35±0.04(13)
(ZS)S	35	23.9±3.9(27)	36	441±74(15)	36	39.48±0.06(20)	36	7.99±0.17(10)	35	1.29±0.07(7)
(ZS)Z	62	10.9±3.1(5)	63	346±58(8)	63	39.35±0.05(1)	63	7.41±0.13(2)	63	1.40±0.05(19)
(ZZx)Z	19	12.5±5.6(7)	20	352±105(9)	18	39.45±0.10(16)	20	7.67±0.22(4)	20	1.44±0.09(27)
(ZxB)B	42	23.7±3.7(25)	50	523±65(20)	50	39.63±0.05(29)	50	10.11±0.15(30)	50	1.57±0.06(31)

(ZC)Z	39	14.9±3.7(13)	43	399±67(11)	43	39.42±0.06(12)	43	8.15±0.15(14)	43	1.37±0.06(15)
3- breedcross										
(BS)Z	20	9.9±5.1(2)	20	520±97(23)	19	39.39±0.08(6)	19	7.82±0.23(8)	19	1.16±0.09(1)
(ZB)S	97	21.3±2.5(21)	114	520±44(22)	113	39.43±0.04(13)	114	8.38±0.10(17)	114	1.31±0.04(9)
(ZZx)S	35	12.9±4.0(8)	35	466±76(18)	35	39.47±0.06(17)	35	8.02±0.17(12)	35	1.45±0.07(28)
(ZC)S	23	34.7±4.7(31)	28	700±82(29)	27	39.35±0.07(3)	27	8.88±0.19(24)	27	1.43±0.07(24)
Z(BS)	37	20.0±3.8(20)	39	511±71(21)	39	39.47±0.06(18)	39	7.86±0.16(9)	38	1.22±0.06(3)
S(ZC)	25	23.8±4.7(26)	31	460±80(17)	31	39.43±0.07(14)	31	8.83±0.18(23)	31	1.34 ±0.07(11)
F_1 x F_1										
(ZB)(SZ)	30	16.4±4.3(15)	45	302±67(4)	44	39.35±0.06(2)	44	8.20±0.15(15)	44	1.29±0.06(6)
(ZS)(SZ)	51	17.5±3.4(17)	65	527±58(25)	64	39.44±0.05(15)	64	8.00±0.13(11)	64	1.36±0.05(14)
(ZS)(ZC)	28	21.7±4.5(23)	33	293±80(3)	32	39.39±0.07(5)	33	8.43±0.18(18)	33	1.37±0.07(16)
(BS)(ZC)	23	21.5±4.7(22)	27	373±83(10)	27	39.54±0.07(26)	27	9.01±0.19(25)	27	1.24±0.07(4)

Table 5. Crossbreeding parameters for adaptive and temperament traits of various breed groups under study

a-additive, m-maternal, dD-direct dominance, mD –maternal dominance, II – indicine breed crosses, TI – taurine and indicine breed crosses, TT – taurine breed crosses, breed groups as given in Table 1; traits as defined in Table 2; negative effects are desirable for adaptive traits and positive effects are desirable for temperament

	TICK	EPG	TEMP	COAT	FT
aS	2.4±3.3	252±60**	-0.21±0.05**	-2.37±0.14**	-0.13±0.05*
aZx	-14.7±5.6**	-90±106	-0.28±0.09**	-2.21±0.25**	0.01±0.09
aZ	-21.6±3.0**	-181±55**	-0.32±0.05**	-4.09±0.13**	-0.16±0.05**
aC	21.7±5.6**	-76±99	0.03±0.09	1.25±0.23**	0.01±0.09
mS	-1.7±3.0	-92±54	-0.05±0.05	-0.36±0.13**	0.13±0.05**
mZx	-0.9±4.1	-29±77	-0.05±0.07	-0.69±0.18**	0.08±0.07
mZ	3.4±2.6	-130±48**	-0.12±0.04**	-0.48±0.11**	0.18±0.04**
mC	2.6±6.8	311±121**	-0.07±0.10	0.17±0.29	0.14±0.11
dD_{II}	0.8±2.4	-36±45	0.01±0.04	-0.13±0.10	-0.03±0.04
dD_{TI}	-5.5±1.3**	-80±24**	-0.06±0.02**	-0.60±0.06**	-0.08±0.02**
dD_{TT}	-7.7±2.6**	-71±47	-0.13±0.04**	-0.91±0.11**	-0.10±0.04*
mD_{II}	-1.5±3.4	-54±64	0.02±0.06	0.13±0.15	0.08±0.06
mD_{TI}	1.1±1.4	-80±25**	-0.07±0.02**	-0.30±0.06**	0.01±0.02
mD_{TT}	-0.8±3.7	-55±69	-0.09±0.06	-0.59±0.16**	-0.09±0.06

*P<0.05, **P<0.01

Table 6. Heterosis percentages for selected F_1 genotypes for various adaptive and temperament traits

Genotypes as given in Table 4; traits as defined in Table 2; negative heterosis is desirable for adaptive traits and positive heterosis is desirable for FT.

Genotype	TICK	EPG	TEMP	COAT	FT
BS / SB	-35*	-10	-0.26	-9.1**	-6.0*
ZB / BZ	-40**	-20*	-0.32**	-11.6**	-6.6*
ZS / SZ	-24	-16*	-0.01	-3.4**	-5.6
ZZx / ZxZ	7	-9	0.04	-1.1	0.3

*P<0.05, **P<0.01

Table 7. Effect of treatment on live weight gain (LWG) of various genotypes under study

Differences between breeds (within treated and control groups) of >11.2 kg (based on overall standard error of difference) are statistically ($P<0.05$) significant; genotypes as given in Table 4; LWG as defined in Table 2; response estimated as treated LWG mean minus control LWG mean

Genotype	N	LWG treated (kg)	LWG Control (kg)	response
Overall	2475	129±1.1	113±1.1	16**
Purebreds				
BB	278	112±1.8	88±1.9	24**
SS	218	131±2.0	105±2.1	26**
ZxZx	50	127±4.1	112±3.9	15**
ZZ	266	127±1.9	117±1.8	10**
F_1				
BS	45	118±4.3	103±4.1	15**
SB	20	123±6.7	92±6.3	31**
BZ	89	137±3.1	126±3.0	11**
ZB	108	135±2.8	122±2.7	13**
SZ	133	138±2.6	123±2.5	15**
ZS	167	140±2.3	123±2.2	17**
ZZx	50	124±4.2	124±4.0	0
ZxZ	100	129±2.9	120±2.9	9*
ZxS	52	127±3.9	110±3.9	17**
ZC	90	146±3.1	133±2.9	13**
F_1backcross				
(ZB)B	56	121±4.0	102±3.6	19**
(ZB)Z	119	120±2.6	108±2.7	12**
(ZS)S	35	133±5.0	111±4.6	22**
(ZS)Z	63	130±3.8	115±3.6	15**
(ZZx)Z	17	132±6.9	117±8.1	15
(ZxB)B	49	112±4.2	91±4.1	21**
(ZC)Z	43	134±4.9	115±3.9	19**
3-breedcross				
(BS)Z	19	132±6.3	115±6.6	17
(ZB)S	111	124±2.8	108±2.7	16**
(ZZx)S	35	142±4.7	121±4.9	21**
(ZC)S	27	129±5.1	116±5.7	13
Z(BS)	39	132±4.2	118±4.8	14*
S(ZC)	29	135±5.3	113±5.2	22**
F_1 x F_1				
(ZB)(SZ)	44	133±4.3	108±4.2	25**
(ZS)(SZ)	64	119±3.4	107±3.8	12**
(ZS)(ZC)	32	132±5.0	113±5.3	19**
(BS)(ZC)	27	132±5.1	119±5.7	13

*$P<0.05$, **$P<0.01$

Table 8. Crossbreeding parameters of live weight gain (LWG) for treated and control animals

a-additive, m-maternal, dD-direct dominance, mD –maternal dominance, II – indicine breed crosses, TI – taurine and indicine breed crosses, TT – taurine breed crosses, breed groups as given in Table 1; LWG as defined in Table 2

	LWG (treated, kg)	LWG (control, kg)
aS	15.3±4.4**	15.2±4.0**
aZx	7.3±7.8	28.5±6.8**
aZ	13.9±4.0**	28.2±3.6**
aC	30.8±7.0**	26.2±6.5**
mS	-0.3±4.0	-2.5±3.5
mZx	-0.4±5.6	-11.3±5.0*
mZ	-1.0±3.5	-1.6±3.1
mC	0.8±8.8	-5.1±7.6
dD_{II}	1.8±3.2	8.2±2.9**
dD_{TI}	11.4±1.7**	15.2±1.5**
dD_{TT}	0.3±3.4	3.4±3.1
mD_{II}	4.1±4.5	0.9±4.3
mD_{TI}	-5.8±1.8**	-5.5±1.6**
mD_{TT}	-2.3±4.7	2.0±4.6

*P<0.05, **P<0.01

Table 9. Phenotypic correlations among adaptive and temperament traits and live weight gain

The values in the upper diagonal represent Zebu breed (ZZ) and lower diagonal represent British breed (BB); traits as defined in Table 2; standard errors ranged between 0.06 and 0.07

	TICK	EPG	TEMP	COAT	FT	LWG
TICK		-0.03	0.01	0.08	-0.05	0.06
EPG	-0.05		0.03	-0.003	0.07	0.04
TEMP	0.12	0.04		0.07	-0.18	-0.08
COAT	0.13	-0.03	0.39		0.09	-0.13
FT	0.01	0.16	-0.15	0.05		0.05
LWG	-0.02	0.001	-0.35	-0.35	-0.01	

4.3 Appendix 3.

OPTIMISATION OF BREED PROPORTIONS IN TROPICALLY ADAPTED BEEF COMPOSITES BASED ON GROWTH AND RESISTANCE TRAITS

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SUMMARY

Data from a crossbreeding study involving crosses of British, Sanga, Zebu cross, Zebu and Continental origins were analysed to estimate direct and maternal additive and dominance effects of growth (weights at weaning and 18 months) and resistance (tick and worm egg counts) traits. The crossbreeding parameters and their respective economic weights were used to derive optimal breed proportions in composites for tropical environments at low, medium and high parasite challenge. A decrease in Continental and increase in Zebu breed proportions was observed in optimal composites with increased parasite challenge.

Keywords: composites, breed proportions, crossbreeding, beef cattle, genetic effects

INTRODUCTION

Systematic crossbreeding or the production of composites are the best ways of exploiting both additive and non-additive gene action in beef cattle. Once established, composites can be maintained as a straightbred population and hence have an advantage over systematic crossbreeding. Newman *et al.* (1998) described the optimisation of breed proportions in tropical environments based on growth traits alone. Hayes *et al.* (2000) stated that optimal composites based on growth traits alone might not represent the true economic merit of the composite. Resistance to ticks and worms plays an important role in determining growth and survivability in the tropics. Hence, this information should be included in optimisation models. In the present study, an attempt is made to optimise breed proportions of a tropically adapted beef composite utilising both growth and resistance traits.

MATERIALS AND METHODS

Animals and experimental design. Data were derived from a crossbreeding study conducted during 1992 – 97 at the National Cattle Breeding Station, 'Belmont', Rockhampton. Breeds of 2608 animals were grouped into British (B), Sanga (S), Zebu cross (Zx), Zebu (Z) and Continental (C) based on their origins and similarities to derive 31 genotypes. Live weights recorded at weaning (WWT) and at around 18 months of age (FWT) were used in the present study. After weaning, calves from each crop were allocated randomly within sex, breed, sire and previous lactation status of the dam into either a treated or a control group. Animals in the treated group were treated regularly every 3 weeks from around 8 months to 18 months of age with anthelmintic to control gastrointestinal nematodes. If ticks were present, all treated animals were dipped in a plunge dip containing acaricide. Tick (TICK) and worm egg (EPG) counts were recorded on all weaned animals every 3 weeks over a 9-week period before commencement of the treatment. After ~8 months of age, TICK and EPG were recorded on control animals at various postweaning ages until 18 months. Further information on breed pooling and treatments is given in Prayaga (2003a, b).

Estimation of crossbreeding parameters. Direct additive (a), maternal additive (m), direct dominance (dD) and maternal dominance (mD) effects of various breed groups under study for WWT, FWT (treated), FWT (control), TICK and EPG were derived. Because all crosses to derive specific dominance effects were not available, genotypes were again regrouped into *Bos indicus* x *Bos indicus* (II), *Bos taurus* x *Bos indicus* (TI) and *Bos taurus* x *Bos taurus* (TT) to facilitate the estimation of dD and mD effects. For this grouping B, S and C were regarded as *Bos taurus* breeds and Z and Zx were regarded as *Bos indicus* breeds. ASREML (Gilmour *et al.* 2002) was used to fit the model:

$$Y_{ij} = \mu + F + b_1 A + b_2 M + b_3 DD + b_4 MD + e_{ij}$$

where Y_{ij} is the jth observation on the ith animal, μ is the least squares mean of the British breed group, F are all the fixed effects such as contemporary group (month – year of birth and age of the dam) and sex and previous lactation status of the dam as a covariate, b_1 and b_2 are the partial regression coefficients for a and m effects of S, Zx, Z and C expressed as a deviation from B mean, b_3 and b_4 are the partial regression coefficients for dD and mD effects, A and M are the fractional coefficients of direct and maternal additive effects of S, Zx, Z and C breed groups, DD and MD are the fractional coefficients of direct and maternal dominance effects for II, TI and TT crosses and e_{ij} is the random error. The fractional coefficients of genetic effects for various genotypes were given by Prayaga (2003a).

Optimisation of breed proportions. Optimal breed proportions (P) for maximum net merit were obtained (Lin, 1996) as : $P = (u'T^{-1}u)^{-1}T^{-1}u$. $T = 1/2(Avu' + uv'A' + Mvu' + uv'M') + H + Q$, where A is a matrix of direct additive effects, M is a matrix of maternal additive effects, $H = \sum_{i=1}^{t} v_i H_i$ where H_i is the direct dominance effects matrix for ith trait and $Q = \sum_{i=1}^{t} v_i Q_i$ where Q_i is the maternal dominance effects matrix for ith trait. u is a vector of ones and v is a vector of economic weights. Economic weights of 0.092 for WWT and 0.241 for FWT as reported by Newman *et al.* (1998) were used in the present study. Optimal breed proportions were derived assuming various TICK (-0.05, -0.25, -0.50) and EPG (-0.005, -0.025, -0.050) economic weights for low, medium and high parasite challenge, as economic weights were not available for tick and worm egg counts in the literature. Low, medium and high parasite challenges were only differentiated by the assumed economic weights and the same parameters were used in the optimisation across all levels of assumed parasite challenge. Though TICK and EPG were assumed to have equal net economic impact, because of the differences in the magnitude of mean TICK and EPG counts, economic weights for EPG were given 1/10th value of those of TICK at each level.

RESULTS AND DISCUSSION

Crossbreeding parameters. Genetic effects for growth and resistance traits are presented in Table 1. High direct additive effects of C and Z breed groups and high positive dominance effects of taurine – indicine crosses (dD$_{TI}$) were evident for growth traits. Z and Zx breed groups showed significantly negative (favourable) additive effects for resistance traits. These crossbreeding parameters were discussed in detail by Prayaga (2003a, b). The important observation in the present study is the difference in the parameters of FWT between treated and control groups. The magnitude of aZ was high in the control group compared to the treated group whereas the magnitude of aC remained the same. mZ was significant in the control group with relatively higher magnitude emphasising the importance of the Zebu breed group in the presence of parasites. The significant and high dD$_{II}$ and mD$_{TI}$ effects in the control group relative to the treated group for FWT stress the importance of indicine breeds in exploiting the hybrid vigour in the presence of parasite challenge.

Table 1. Crossbreeding parameters for growth and parasite resistance in various breed groups

	WWT	FWT (treated)	FWT (control)	TICK	EPG
Direct additive					
aS	16.4±3.0	33.2±6.9	41.6±6.2	2.4±3.3	252±60
aZx	7.8±5.2	23.5±12.2	30.9±10.6	-14.7±5.6	-90±106
aZ	16.0±2.8	36.1±6.4	49.4±5.6	-21.6±3.0	-181±55
aC	46.4±4.9	79.5±11.1	76.1±10.1	21.7±5.6	-76±99
Maternal additive					
mS	9.9±2.7	8.6±6.3	3.3±5.5	-1.7±3.0	-92±54
mZx	14.7±3.8	9.0±8.8	7.1±7.8	-0.9±4.1	-29±77
mZ	13.3±2.4	8.3±5.6	12.0±4.9	3.4±2.6	-130±48
mC	4.3±6.0	-0.6±13.9	2.6±11.9	2.6±6.8	311±121
Direct dominance					
dD_{II}	5.8±2.2	6.8±5.1	15.7±4.6	0.8±2.4	-36±45
dD_{TI}	11.4±1.2	26.1±2.7	26.9±2.4	-5.5±1.3	-80±24
dD_{TT}	6.2±2.3	8.0±5.3	7.3±4.8	-7.7±2.6	-71±47
Maternal dominance					
mD_{II}	1.4±3.2	2.8±7.1	8.8±6.7	-1.5±3.4	-54±64
mD_{TI}	15.7±1.3	5.2±2.9	9.1±2.6	1.1±1.4	-80±25
mD_{TT}	5.8±3.4	0.7±7.5	6.7±7.1	-0.8±3.7	-55±69

Optimal breed proportions. When only growth traits were considered for optimisation, the control group optimal breed proportions in the composite were 36% and 64% for Z and C respectively (Table 2). This was comparable to two-breed optimal composite of Brahman (32%) and Charolais (68%) suggested by Newman *et al.* (1998). Based on treated group genetic parameters, an increase in the proportion of C and decrease in Z was evident with optimal breed proportions of 24.4% and 75.6% of Z and C respectively.

While optimising breed proportions using growth and resistance traits, treated group FWT parameters were used as they represented actual growth genetic components in the absence of parasites. At very low TICK, EPG or both the optimal breed proportions of Z in the composite ranged between 30.0 – 37.7% and the C proportions ranged between 62.3 – 70.0% indicating only slight deviation from the optimal proportions derived from growth traits alone. At medium tick levels, the C breed proportion reduced to 49.2% and Z proportion increased to 50.8%. Hence, at medium tick levels, optimal breed proportions derived by including tick count information reduces the non adapted breed proportion to <=50% even without constraining its proportion as described by Hayes *et al.* (2000). At high tick levels alone or at medium or high tick and worm infestations, S entered into optimal breed proportions. As the S breed group had high faecal egg counts (Prayaga 2003b), its proportion in the optimal composite was high only when growth + TICK were considered. But its proportions reduced when both TICK and EPG were considered along with growth traits. At high tick and worm levels, the Zebu breed (91.9%) was the predominant component of the optimal composite together with Sanga (8.1%). The Continental breed group was no longer represented in the optimal composite because the negative influence of high tick and worm egg counts outweighed the growth benefits.

Further studies to derive economic weights for tick and worm egg counts at various levels of parasite challenge could provide more accuracy to these evaluations. The present study assumed the availability of all possible breed groups while deriving the optimal composites, but it can also be utilised in more practical situations where only particular breeds are available to develop tropically adapted composites. In that situation, additional traits such as fertility and product quality would also need to be considered in the derivation of optimal composites for the tropics and sub-tropics.

Table 2. Breed proportions in optimal composites under various levels of parasite challenge

	Economic weights				Breed Proportions		
Traits	WWT	FWT	TICK	EPG	S	Z	C
I. Growth traits							
a. WWT+FWT (treated)	0.092	0.241	-	-	-	24.4	75.6
b. WWT+FWT (control)	0.092	0.241	-	-	-	36.0	64.0
II.Growth traits + TICK							
Low	0.092	0.241	-0.05	-	-	30.0	70.0
Medium	0.092	0.241	-0.25	-	-	50.8	49.2
High	0.092	0.241	-0.50	-	18.7	66.7	14.6
III. Growth traits + EPG							
Low	0.092	0.241	-	-0.005	-	32.6	67.4
Medium	0.092	0.241	-	-0.025	-	56.0	44.0
High	0.092	0.241	-	-0.050	-	73.6	26.4
IV. Growth traits +TICK +EPG							
Low	0.092	0.241	-0.05	-0.005	-	37.7	62.3
Medium	0.092	0.241	-0.25	-0.025	3.9	72.0	24.1
High	0.092	0.241	-0.50	-0.050	8.1	91.9	-

S - Sanga, Z – Zebu and C – Continental

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