

# Importance of adaptation and genotype $\times$ environment interactions in tropical beef breeding systems

H. M. Burrow<sup>†</sup>

Cooperative Research Centre for Beef Genetic Technologies, UNE, Armidale NSW 2351, Australia

(Received 28 December 2010; Accepted 22 November 2011; First published online 17 January 2012)

*This paper examines the relative importance of productive and adaptive traits in beef breeding systems based on Bos taurus and tropically adapted breeds across temperate and (sub)tropical environments. In the (sub)tropics, differences that exist between breeds in temperate environments are masked by the effects of environmental stressors. Hence in tropical environments, breeds are best categorised into breed types to compare their performance across environments. Because of the presence of environmental stressors, there are more sources of genetic variation in tropical breeding programmes. It is therefore necessary to examine the genetic basis of productive and adaptive traits for breeding programmes in those environments. This paper reviews the heritabilities and genetic relationships between economically important productive and adaptive traits relevant to (sub)tropical breeding programmes. It is concluded that it is possible to simultaneously genetically improve productive and adaptive traits in tropically adapted breeds of beef cattle grazed in tropical environments without serious detrimental consequences for either adaptation or production. However, breed-specific parameters are required for genetic evaluations. The paper also reviews the magnitude of genotype  $\times$  environment (G  $\times$  E) interactions impacting on production and adaptation of cattle, where 'genotype' is defined as breed (within a crossbreeding system), sire within breed (in a within-breed selection programme) or associations between economically important traits and single nucleotide polymorphisms (SNPs – within a marker-assisted selection programme). It is concluded that re-ranking of breeds across environments is best managed by the use of the breed type(s) best suited to the particular production environment. Re-ranking of sires across environments is apparent in poorly adapted breed types across extreme tropical and temperate environments or where breeding animals are selected in a temperate environment for use in the (sub)tropics. However, G  $\times$  E interactions are unlikely to be of major importance in tropically adapted beef cattle grazed in either temperate or (sub)tropical environments, although sex  $\times$  environment interactions may provide new opportunities for differentially selecting to simultaneously improve steer performance in benign environments and female performance in harsher environments. Early evidence suggests that re-ranking of SNPs occurs across temperate and tropical environments, although their magnitude is still to be confirmed in well-designed experiments. The major limitation to genetic improvement of beef cattle over the next decade is likely to be a deficiency of large numbers of accurately recorded phenotypes for most productive and adaptive traits and, in particular, for difficult-to-measure adaptive traits such as resistance to disease and environmental stressors.*

**Keywords:** beef cattle, adaptation, production, genotype  $\times$  environment interactions

## Implications

In beef breeds that are well adapted to their production environments, there are no apparent constraints to simultaneous genetic improvement of productive and adaptive traits to maximise profitability of herds grazed in the (sub)tropics, although breed-specific parameters are required for genetic evaluations. G  $\times$  E interactions are unlikely to be of major

importance in tropically adapted cattle grazed in either temperate or (sub)tropical environments, although re-ranking is likely to occur in temperate breeds of cattle reared in temperate and (sub)tropical environments. Genomic selection based on single nucleotide polymorphisms offers new opportunities for commercial breeders to better breed and manage their cattle in future. However, the current major limitation to genetic improvement of beef cattle (in all environments) is the lack of large numbers of accurately recorded phenotypes for most productive and adaptive traits.

<sup>†</sup> E-mail: Heather.Burrow@une.edu.au

## Introduction

Livestock produce ~30% of the agricultural gross domestic product (GDP) in the developing world and ~40% of global agricultural GDP (World Bank, 2009). Most livestock production in the developing world occurs in tropical and subtropical areas, collectively referred to herein as the (sub)tropics. Global cattle inventories estimate ~1.5 billion head of cattle, with more than 65% located in the (sub)tropics (Morgan and Tallard, 2007). Payne and Hodges (1997) suggest that beef cattle breeders in developed countries depend primarily on use of additive genetic variance with some limited use of heterosis to achieve genetic improvement. In the (sub)tropics, additive genetic variance and heterosis are equally important for genetic improvement. However, in developing (sub)tropical countries, cattle breeders are generally not able to capture gains through additive genetic variance because of the difficulty of measuring and directly comparing the performance of their animals. Further, because of the variable environmental conditions in the (sub)tropics, the possibility of genotype  $\times$  environment ( $G \times E$ ) interactions affecting genetic merit for economically important traits must be considered.

Cattle grazed at pasture in (sub)tropical environments are subjected to numerous stressors including ectoparasites (cattle ticks; horn flies, buffalo flies, screw-worm and tsetse flies; other biting insects), endoparasites (gastrointestinal helminths or worms), seasonally poor nutrition, high heat and humidity and diseases often transmitted by parasites. The impact of each stressor on production and animal welfare is often multiplicative rather than additive, particularly when animals are already undergoing physiological stress such as lactation (e.g. Turner and Short, 1972; Turner, 1982; Frisch and Vercoe, 1984; Frisch and O'Neill, 1998). Under extensive production systems common in the (sub)tropics, it is generally not possible to control the stressors through management strategies alone. Even if intervention strategies were feasible, the treatments *per sé* often cause their own problems. For example, chemical treatments to control parasites generate concern about residues in beef products. In addition, the parasites acquire resistance to the chemical treatments, creating additional parasite control problems. In intensive feedlot systems and live cattle exports across (sub)tropical regions, high heat and humidity, even in the absence of other stressors, can become critically important for both production and animal welfare reasons. In such cases, management interventions may be possible, but they are difficult and/or expensive to implement, particularly in poorly adapted cattle. Therefore, the best method of reducing the impacts of these stressors to improve productivity and animal welfare is to breed cattle that are productive in their presence, without the need for managerial interventions.

Maximising beef production and profitability requires matching the 'genotype' to the specific production environment. Here, 'genotype' can be defined as breed (within a crossbreeding system), sire within breed (in a within-breed selection programme) or associations between economically

important traits and single nucleotide polymorphism (SNP) genotypes (within a marker-assisted selection programme).

Some genotypes are better suited to particular environments. However, in every environment, factors limit beef production, meaning no one genotype is best in all environments. This paper examines the relative importance of productive and adaptive traits in beef breeding systems for (sub)tropical environments. It also examines the magnitude of  $G \times E$  interactions in those systems, with the aim of identifying strategies that can be used to mitigate  $G \times E$  where required.

## Breed groupings

Although in temperate environments there may be substantial differences in performance between individual breeds, in (sub)tropical areas, differences in performance are masked by the effects of environmental stressors on productive attributes. As summarised in the review of Burrow *et al.* (2001), for most purposes in the (sub)tropics, breeds can be categorised into general breed types or groupings including:

1. *Bos taurus* (British and Continental);
2. *Bos indicus* (Brahman, Nellore);
3. tropically adapted taurine breeds (southern African Sanga, West African humpless and Criollo breeds of Latin America and the Caribbean);
4. tropically adapted indicine  $\times$  British/Continental composite breeds (e.g. Santa Gertrudis, Braford, Charbray);
5. tropically adapted taurine  $\times$  British/Continental composite breeds (e.g. Bonsmara, Belmont Red, Senepol);
6. East African zebu breeds (e.g. Boran); and
7. the first cross ( $F_1$ ) between *B. indicus* and *B. taurus*, which has attributes that are different from other breed types, particularly in harsher environments.

Comparative rankings of the various breed types for different characteristics in temperate and tropical environments based on the Burrow *et al.* (2001) review are shown in Table 1. Because of the paucity of direct breed-type comparisons from most (sub)tropical areas, the rankings in the (sub)tropics are largely based on results from the Belmont Research Station and from the associated research programmes in northern Australian beef industry herds. Breed-type comparisons in temperate areas are largely derived from the Meat Animal Research Center in Nebraska, USA.

## Relative importance of productive and adaptive traits

In this paper, tropical adaptation is defined as an animal's ability to survive, grow and reproduce in the presence of the endemic stressors of tropical environments. Economic implications for production systems from the lack of adaptation include production losses impacting on both product quantity and quality, mortalities (particularly from endemic diseases transmitted by parasites), treatment costs (where treatment is feasible) and marketing issues, for example, associated with the presence of chemical residues in beef, resulting from treatments to control parasites.

**Table 1** Comparative rankings of different breed types for productive traits in temperate and tropical environments and for adaptation to stressors of tropical environments (Source: Burrow *et al.*, 2001 and references cited therein; the more +s, the higher the value for the trait)

Breed type	<i>Bos taurus</i>		<i>Tropical B. taurus</i>	<i>Bos indicus</i>		F <sub>1</sub> Brahman × British
	British	Continental <sup>E</sup>	Sanga	Indian	African	
Temperate <sup>A</sup>						
Growth	++++	+++++	+++	+++	++	++++
Fertility	+++++	++++	++++	+++	++++	+++++
Tropical <sup>A</sup>						
Growth	++	++	+++	++++	++	++++
Fertility	++	++	+++++	+++	++++	+++++
Mature size	++++	+++++	+++	++++	+++	++++
Meat quality <sup>B</sup>	+++++	++++	+++++	+++	++++	++++
Resistance to environmental stressors						
Cattle ticks <sup>C</sup>	+	+	++++	+++++	+++++	++++
Worms <sup>D</sup>	+++	+++	+++	+++++	++++	++++
Eye disease	++	+++	+++	+++++	++++	++++
Heat	++	++	+++++	+++++	+++++	+++++
Drought	++	+	+++++	+++++	+++++	++++

<sup>A</sup>Temperate environment is assumed to be one free of environmental stressors, whilst tropical environment rankings apply where all environmental stressors are operating. Hence, while a score of, for example, +++++ for fertility in a tropical environment indicates that breed type would have the highest fertility in that environment, the actual level of fertility may be less than the actual level of fertility for breeds reared in a temperate area, due to the effect of environmental stressors that reduce reproductive performance.

<sup>B</sup>Principally meat tenderness.

<sup>C</sup>*Rhipicephalus microplus*.

<sup>D</sup>Specifically *Oesophagostomum*, *Haemonchus*, *Trichostrongylus* and *Cooperia* spp.

<sup>E</sup>Data from purebred Continental breeds are not available in tropical environments and responses are predicted from the CSIRO Rockhampton crossbreeding data.

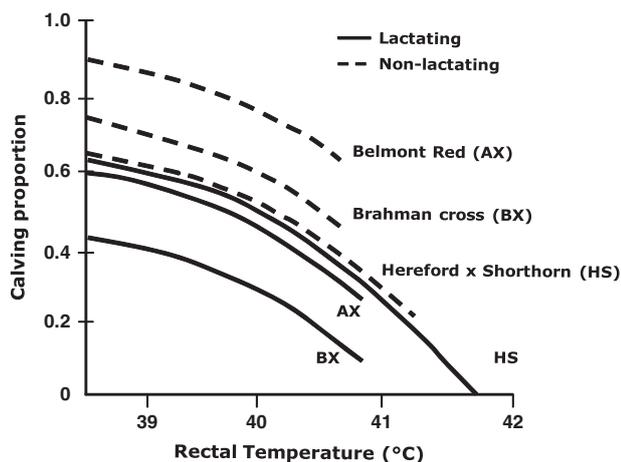
Although temperament, an aspect of cattle behaviour, is not specific to cattle reared in the tropics, it has implications for tropical adaptation because animals reared in extensive environments are generally handled less frequently than those reared in temperate environments. Inherent differences in temperament between individuals are therefore exaggerated because of the lack of routine handling. This means temperament is an important trait for management reasons under the extensive pastoral systems commonly found in the (sub)tropics.

Poor temperament affects the profitability of beef enterprises by increasing production costs, as well as increasing the risk of injury to animals and their handlers. Significant production losses have been associated with poor temperament, particularly in intensive production systems such as feedlots (Burrow and Dillon, 1997; Petherick *et al.*, 2002) and artificial breeding programmes (Burrow *et al.*, 1988). Sires with poor temperament have been shown to produce progeny whose beef is less tender than progeny of sires with better temperaments (Reverter *et al.*, 2003b; Kadel *et al.*, 2006), although Burrow *et al.* (1999) and Wolcott *et al.* (2009) also indicate it may be possible to overcome this negative relationship between temperament and beef tenderness through use of best practice processing techniques. Regardless, with the increasing emphasis placed by consumers on ethical production systems, it is essential to consider the animal welfare implications of handling animals with poor temperaments.

Table 1 presents an aggregated summary of productive and adaptive data from a range of sources (see references in the original Burrow *et al.*, 2001 review). From that table,

it is apparent that in the presence of environmental stressors, productive attributes (primarily growth and fertility) of poorly adapted cattle are significantly reduced relative to their performance in temperate environments or relative to the performance of adapted cattle in the (sub)tropics. Re-ranking of breeds across the different temperate and tropical environments shown in Table 1 is also examined in the following discussion of G × E interactions. However, it is apparent from Table 1 that any breeding programme designed for cattle grazing in the (sub)tropics must consider the impacts of both productive and adaptive attributes, even though adaptive traits (and some productive traits) are generally very difficult and/or expensive to measure.

As described in many previous publications from northern Australia summarised in Table 1, the relative importance of adaptive traits and their impacts on productive traits such as growth (e.g. Frisch and Vercoe, 1984) and calving rates (e.g. Turner, 1982) depend greatly on the breed type, the degree of severity of the individual stressor and whether or not multiple stressors are impacting on performance. For example, Figure 1 shows the relationship between rectal temperatures and calving rates in British, Brahman- and Africander-derived lactating and non-lactating crossbred cows reared at Belmont Research Station in northern Australia. The average depression in calving rates due to susceptibility to heat stress was 0.15 to 0.25 in F3 *et seq.* generation British crossbred cows and 0.10 in the F3 *et seq.* generation *B. indicus* (Brahman) and Sanga (Africander) × British crossbreds. Differences in performance between lactating and non-lactating British cows were much smaller than the differences evident in the Brahman and



**Figure 1** The impact of rectal temperature under conditions of high ambient temperature and calving rates of lactating and non-lactating cows of three breed types (British – Hereford × Shorthorn cross; Brahman × British; Africander × British) grazed at pasture in northern Australia (Source: Turner, 1982).

Africander cross cows (Turner, 1982). These and other results from (sub)tropical environments suggest that breeding programmes in such areas must consider both productive and adaptive traits if they are to be effective. However, the differing impacts of environmental stressors across breed types suggest that economic weightings for use in selection indices will need to be specifically developed for each breed type and environment.

### Are the traits under genetic control?

For traits to be included in effective breeding programmes, they must be under direct or indirect genetic control. Direct genetic control is assessed by estimating the heritability of traits. Indirect genetic control is achieved through favourable or unfavourable associations (genetic correlations) between different traits.

Earlier extensive reviews of the scientific literature (e.g. Davis, 1993; Koots *et al.*, 1994; Burrow, 2001) and the references therein indicate that direct and maternal growth traits at all ages are at least moderately heritable in both temperate and (sub)tropical environments, as well as in temperate and tropically adapted breeds of cattle, meaning they will respond to genetic improvement programmes. The reviews also indicate it is possible to select to improve growth rate and weights of sale progeny while simultaneously restricting calf birth weights and mature cow weights to avoid the negative consequences of dystocia and increased mature cow feed requirements.

Genetic associations exist between growth traits and body composition attributes such as retail beef yield, fat depth and marbling (the review of Burrow *et al.*, 2001 and references therein; Reverter *et al.*, 2003a and 2003b; Wolcott *et al.*, 2009) and feed efficiency (Robinson and Oddy, 2004; Barwick *et al.*, 2009a). Genetic and phenotypic associations also exist between growth and reproductive attributes (Burrow *et al.*, 1991; Burrow, 2001 and references therein).

These associations must be included in the design of breeding programmes for both temperate and (sub)tropical environments.

The Burrow *et al.* (2001) review and references therein indicate that carcass composition traits (e.g. carcass weight, fat thickness and marbling) are moderately to highly heritable. Most estimates of retail beef yield percentage are also highly heritable, offering good potential for within-breed improvement, although a moderate-to-strong antagonistic relationship exists between yield and marbling, meaning that measurement of all traits will be required if unfavourable consequences of selection are to be avoided. Beef tenderness is lowly heritable in British breeds of cattle when processing factors are strictly controlled (Johnston *et al.*, 2003b); however, tenderness is moderately to highly heritable in *B. indicus* breeds (the Burrow *et al.*, 2001 review and references therein; Johnston *et al.*, 2003b; Wolcott *et al.*, 2009), suggesting the trait can be improved in tropically adapted cattle by selection. However, the lack of direct measurement of beef tenderness in live animals remains a constraint for breeding programmes.

Most reviews of the published literature suggest the heritability of female reproductive traits such as pregnancy rate or days to calving is low (e.g. Davis, 1993; Koots *et al.*, 1994; Burrow, 2001 and references therein). However, recent reports indicate the component traits of reproduction (e.g. age at puberty and *post-partum* anoestrus interval) are much more heritable, and therefore potentially much more useful for genetic improvement programmes than traditional measures (Johnston *et al.*, 2006, 2009 and 2010).

Except for a number of largely interdependent Australian studies (see reviews of Kloosterman *et al.*, 1992; Davis, 1993; Prayaga *et al.*, 2006 and references therein), there are relatively few reports of the heritability of resistance to parasites, disease and heat stress in beef cattle. Studies in sheep and beef cattle from Australia and elsewhere attribute differences in host–parasite interactions to genetics based on measured differences between breeds (e.g. Duarte-Ortuño *et al.*, 1988; de Castro and Newson, 1993; Stear and Murray, 1994; Sorci *et al.*, 1997; Stein *et al.*, 2009). The paucity of reports of genetic parameters for adaptive traits is assumed to be because of the great difficulty in measuring the very large numbers of animals required for such studies. This section therefore briefly reviews the scientific literature to determine the extent of genetic control of the recently introduced component traits of female reproduction and adaptive traits, to allow an evaluation of the relative impact of productive and adaptive traits in cattle breeding programmes for (sub)tropical environments.

### Component traits of female reproduction

Because of the low heritability (i.e. <0.10) of most traditional measures of female reproduction, inclusion of female fertility traits in beef genetic evaluation systems may require identification of new traits that can be recorded early in life, are heritable and are genetically correlated with the

**Table 2** Heritabilities ( $h^2$ ) and standard errors (in parentheses) for heifer puberty traits in Brahmans and Tropical Composites (Source: Johnston *et al.*, 2009; CL – corpus luteum; CA – corpus albicans) and for lactation anoestrus traits in Brahmans only (Source: Johnston *et al.*, 2010; PPAI – post-partum anoestrus interval)

Trait	Brahman $h^2$	Tropical Composite $h^2$
Pubertal traits		
Age at first CL/CA	0.57 ( $\pm 0.12$ )	0.52 ( $\pm 0.12$ )
Weight at first CL/CA	0.56 ( $\pm 0.12$ )	0.46 ( $\pm 0.11$ )
Fat depth at first CL/CA	0.55 ( $\pm 0.13$ )	0.39 ( $\pm 0.11$ )
Condition score at first CL/CA	0.22 ( $\pm 0.10$ )	0.16 ( $\pm 0.07$ )
Reproductive tract size	0.03 ( $\pm 0.06$ )	0.20 ( $\pm 0.09$ )
Presence of CL/CA before joining	0.33 ( $\pm 0.10$ )	0.13 ( $\pm 0.07$ )
Presence of CL/CA at the start of joining	0.20 ( $\pm 0.09$ )	0.07 ( $\pm 0.05$ )
Post-partum traits (3-year-old cows)		
PPAI (days)	0.52 ( $\pm 0.14$ )	
PPAI (cows ovulating pre-weaning)	0.11 ( $\pm 0.15$ )	Data not yet published
PPAI (cows ovulating post-weaning)	0.17 ( $\pm 0.20$ )	
Post-partum traits (4-year-old cows)		
PPAI (days)	0.20 ( $\pm 0.12$ )	Data not yet published
PPAI (cows ovulating pre-weaning)	0.04 ( $\pm 0.12$ )	
Post-partum traits (5-year-old cows)		
PPAI (days)	0.24 ( $\pm 0.14$ )	Data not yet published
PPAI (cows ovulating pre-weaning)	0.13 ( $\pm 0.11$ )	

underlying profit trait. One of the aims of a major study in northern Australia (Burrow *et al.*, 2003) was to identify alternative measures of female reproduction and their associations with other productive and adaptive traits in tropical cattle. The study compared Brahman and Tropical Composite heifers raised in four locations in northern Australia from weaning until they entered the breeding herds at ~27 months of age, and subsequently had the opportunity to raise six calves before being culled at around 10 years of age. Each heifer was ovarian scanned every 4 to 6 weeks from weaning until she entered the breeding herd to determine the age at first-observed *corpus luteum* (CL) or *corpus albicans* (CA). The presence of a CL/CA was used to define the age at puberty for each heifer. Reproductive tract size was also measured at the start of the first joining period (Johnston *et al.*, 2009).

In females that had calved, ovarian ultrasound scanning for the presence of a CL/CA was also used to determine resumption of cycling *post partum*. Scanning of all cows commenced at the end of the calving period (coinciding with the start of mating) when the cows were on average 6 to 7 weeks *post partum* and was continued every 4 weeks up to weaning, 6 to 7 months after the start of mating. Those cows still without an observed CL/CA at weaning were scanned every 4 to 8 weeks until their first CL/CA was observed. Several traits were defined for lactating cows to investigate the degree of genetic control of *post-partum* lactation anoestrus. The first trait, describing the *post-partum* anoestrus interval (PPAI), was defined as the number of days from commencement of scanning to the estimated first ovulation date for each cow as defined by the presence of a CL/CA and from estimates of foetal age for pregnant cows. Distributions of PPAI records revealed a spike after weaning. Hence, to

further investigate PPAI, the measure was divided into two traits, representing cows that first ovulated before weaning and those that first ovulated post weaning. The post-weaning trait was re-computed as the number of days from the weaning date to the estimated first ovulation date. Each of the traits was defined for lactating 3-, 4- and 5-year-old cows (Johnston *et al.*, 2010). To date, results for lactating cows have been published only for Brahmans, because of the greater incidence of *post-partum* anoestrus evident in that breed. Complete results will be submitted for publication in early 2012.

In contrast to heritabilities of  $<0.10$  for most traditional reproductive traits, Johnston *et al.* (2009) report that several pubertal traits such as age, weight and fat depth at time of first CL/CA were moderately to highly heritable (Table 2). In general, more genetic variation was observed for Brahmans than for Tropical Composites. Genetic differences observed for age at first CL/CA in Brahmans appear to be more important than those for Tropical Composites because of the lower percentage of Brahman heifers observed with a CL/CA before joining.

Genetic correlations between the age at CL/CA and both heifer- and steer-production traits showed important genotype differences (Johnston *et al.*, 2009), but the authors concluded that selection could be used to change heifer age at puberty in both Brahmans and Tropical Composites, with few major antagonisms with either steer- or heifer-production traits. Results across the four different tropical locations indicate that puberty in beef heifers is not simply controlled by weight, growth rate or age alone, but appears to involve a combination of factors relating to physiological age, size and growth rate and probably also involves body condition in Brahmans.

**Table 3** Range of heritabilities ( $h^2$ ) for traits associated with resistance of cattle to stressors of tropical environments (note: except for measures of temperament, these estimates are almost exclusively derived from experiments in cattle grazed at pasture in Northern Australia)

Source	Trait/measurement	$h^2$
Prayaga <i>et al.</i> (2006 – review)	Resistance to ticks – number of ticks on one side of the animal	0.39 to 0.44
Prayaga <i>et al.</i> (2009)	Resistance to ticks – score (0 to 5 scale) of number of ticks on one side of the animal	0.09 to 0.05
Prayaga <i>et al.</i> (2006 – review)	Resistance to worms – worm egg count per gram of faeces	0.24 to 0.57
Prayaga <i>et al.</i> (2009)	Resistance to worms – worm egg count per gram of faeces	0.28 to 0.40
Prayaga <i>et al.</i> (2006 – review)	Resistance to buffalo flies – number of flies on one side of the animal	0.06 to 0.36
Prayaga <i>et al.</i> (2009)	Resistance to buffalo flies – fly lesion score on a 1 to 5 scale	0.04 to 0.19
Prayaga <i>et al.</i> (2006 – review)	Resistance to heat stress – rectal temperature under conditions of heat stress	0.12 to 0.33
Prayaga <i>et al.</i> (2009)	Resistance to heat stress – rectal temperature under conditions of heat stress	0.21 to 0.22
Prayaga <i>et al.</i> (2006 – review)	Resistance to heat stress – coat score on a 1 to 7 scale	0.08 to 0.26
Prayaga <i>et al.</i> (2009)	Resistance to heat stress – coat score on a 1 to 7 scale	0.09 to 0.14
Burrow (1997 – review)	Temperament – unrestrained measures, including flight distance and flight time	0.18 to 0.70
Burrow (1997 – review)	Temperament – restrained measures, including crush score	0.0 to 0.67
Prayaga <i>et al.</i> (2006 – review)	Temperament – unrestrained measures (flight distance or flight time)	0.20 to 0.70
Prayaga <i>et al.</i> (2009)	Temperament – flight time	0.17 to 0.31

Tick burdens in the Prayaga *et al.* (2009) study were very low due to prolonged periods of drought.

Burrow (1997) reports a wide range of measures from studies around the world that were focused mainly on temperament, whereas the Prayaga *et al.* (2006) review is restricted to measures of flight time in animals that were simultaneously recorded for productive and adaptive traits.

In lactating Brahman cows derived from the same experiment, Johnston *et al.* (2010) reported that calving rates were reduced relative to non-lactating cows, especially in 3-year-old cows. This was evident in their mean PPAI of 134 days, with only 53% of 3-year-old cows having their first ovulation before the weaning of their first calf. For lactating 4- and 5-year-old cows, the PPAI averaged 66 and 40 days with 81% and 93% recording an ovulation before weaning, respectively. For cows cycling before weaning, the average PPAI declined across age classes from 40 days for 3-year-old cows to 36 days for 5-year-old cows. For those cows not observed with a CL/CA before weaning, the average number of days from weaning until their first ovulation was 99, 74 and 76 for 3-, 4- and 5-year-old cows, respectively. Heritabilities of PPAI were highest (0.52) in 3-year-old cows, declining to 0.20 and 0.24 in lactating 4- and 5-year-old cows (Table 2). Results suggest that much of the genetic variance in PPAI is the result of whether or not the cow cycled before weaning. Primary reasons for delayed *post-partum* resumption of cycling are low body condition (Rudder *et al.*, 1985) and the effect of suckling (Montiel and Ahuja, 2005). Until the complete dataset from six calving opportunities has been analysed, firm recommendations about which trait(s) has the most potential for use in breeding programmes cannot be made. Ideally, the complete analyses will identify early-life indicator traits that can be used to improve lifetime reproductive performance.

#### Adaptive traits

Stear *et al.* (2001) reviewed the livestock production literature and reported that, across species, the heritability of traits associated with resistance to many important diseases and parasites is often high and considerable variation exists among animals. Their review did not differentiate between livestock reared in temperate and tropical environments or

under extensive and intensive production systems. Among ectoparasites in cattle, they reported significant heritabilities for nematode species (Stear *et al.*, 1990; Mackinnon *et al.*, 1991, both based on a subset of data from northern Australia reported herein); tick infestations (Stear *et al.*, 1990; Minjauw and de Castro, 2000); and buffalo fly numbers (Stear *et al.*, 1990). Among endoparasites, they reported significant heritabilities for resistance to trypanosomes (Murray *et al.*, 1991) and also indicated the heritability of immune response traits could be substantial in pigs and dairy cattle.

Prayaga *et al.* (2006) undertook a review of the genetics of tropical adaptation just in beef cattle, summarising the genetic basis of adaptive traits and their relationships with productive attributes. They indicated that most adaptive traits were moderately to highly heritable (Table 3). Their results were confirmed in a later, independent experiment undertaken in similar environments to the studies in the earlier review (Prayaga *et al.*, 2009), indicating there is ample opportunity to improve these traits through selection, even though they are difficult to include in genetic evaluation systems because of their difficulty of measurement.

On the basis of the genetic correlations amongst the various adaptive traits, it appears that selection to improve resistance to any one stressor is likely to increase resistance to other stressors (Burrow, 2001; Burrow and Prayaga, 2004; Prayaga *et al.*, 2006). This is particularly true for resistance to ticks, worms and heat stress, where genetic correlations have been shown to be consistently moderately positive, suggesting the same or closely linked genes affect these traits.

The same is not true of correlations between adaptive and productive traits. Except for heat stress measured by rectal temperatures under conditions of high ambient temperatures, resistance to most environmental stressors appears to be largely independent of productive traits such as growth, reproduction and product quality, albeit the conclusions

are drawn from a small number of largely interdependent Australian studies (Burrow, 2001). Genetic correlations between resistance to heat stress and growth and reproduction traits (Turner, 1982 and 1984; Burrow, 2001; Burrow and Prayaga, 2004) are generally significantly negative (favourable), emphasising there are many genes in common between genes controlling growth and reproduction in the tropics and rectal temperatures when ambient temperatures are high.

On the basis of this review, most economically important productive and adaptive traits are at least moderately heritable, indicating they will respond to selection. In addition, there are no major strongly antagonistic relationships between the traits that would preclude simultaneous genetic improvement for all the traits in tropical beef breeding objectives.

### $G \times E$ interactions

$G \times E$  interactions may impact significantly on production levels across different environments. Such interactions have traditionally been indicated by the re-ranking of breeds, or sires within breeds, for performance across different environments or by genetic correlations between traits in different environments that are either antagonistic, or if positive, somewhat less than unity (e.g.  $<0.80$ ). More recently, interest has focused on possible changes in SNP associations with economically important traits across environments as a further indication of  $G \times E$ . This section examines each of the different methods of evaluating the magnitude of  $G \times E$  interactions, particularly as they impact on breeding programmes in the (sub)tropics.

#### *Re-ranking of breeds across environments*

Table 1 suggests re-ranking of breeds can be routinely expected to apply across extreme temperate and (sub)tropical environments. Burrow *et al.* (2001) and Burrow (2006) cite many earlier studies from a number of countries, which report that differences between breeds are significant and large for most economically important traits. However, the ranking of the breeds for those traits is not always consistent across environments. In the (sub)tropics, the easiest way for commercial beef producers to overcome  $G \times E$  interactions without managerial intervention is simply to use the most appropriate breed(s), that is, those that are best adapted to the stressors of the particular environment. In within- or across-breed selection programmes, this allows optimal exploitation of the significant between-breed differences to maximise production levels, without compromising adaptation to the environment. For beef production in (sub)tropical environments, it makes little sense to use purebred British or Continental breeds of cattle unless they have specific attributes that mean the cost of using them in those (sub)tropical environments is well compensated by financial rewards through niche markets.

#### *Re-ranking of sires within breeds*

$G \times E$  interactions that involve re-ranking of sires within breeds across environments potentially have a much greater impact on beef production than re-ranking of breeds *per sé*.

This is because it is much simpler and less expensive to change to a better adapted breed in (sub)tropical environments than it is to identify sires within breed(s) that are genetically superior for the full range of productive and adaptive traits required in these environments. For example, if breeders aim to improve beef tenderness in tropically adapted cattle, it is far easier to use tropically adapted breed types that have inherently more tender beef (e.g. the tropically adapted taurine breeds) than to select within the *B. indicus* breeds to improve tenderness, at least using traditional quantitative genetic approaches. In future, the use of DNA markers may make within-breed selection more feasible. It is important to independently examine the extent of  $G \times E$  in both poorly adapted (British and Continental) and tropically adapted breeds.

*Re-ranking of British breed sires across temperate and tropical environments.* Frisch (1981) compared Hereford  $\times$  Shorthorn (HS) cattle selected for high growth in the presence of environmental stressors in the Australian tropics relative to a control line of HS cattle that had been selected at random. Selection for high growth in HS cattle increased adaptation to environmental stressors, but did not increase components associated with direct genes for growth. Selected animals grew faster in the presence of stressors, but control animals grew faster in their absence, suggesting that improvements in growth rate were achieved *entirely* through increases in resistance to environmental stressors that affected growth rate.

In contrast, Rudder *et al.* (1986) compared progeny of the same HS control line sires selected in the presence of environmental stressors with progeny of commercial sires selected in the absence of parasites and reared together in the (sub)tropics. They concluded that re-ranking of sires for growth did not occur across tropical and temperate environments if the sires were selected in tropical environments. However, considerable re-ranking ( $G \times E$ ) occurred if bulls were selected in more benign environments and then used in harsher environments.

In the United States of America, the extent of  $G \times E$  was studied for pre- and post-weaning traits of Hereford bulls and heifers and reproductive traits of females bred in Montana and raised in Montana and Florida (Burns *et al.*, 1979; Koger *et al.*, 1979; Pahnish *et al.*, 1983 and 1985). Results indicated the existence of economically important  $G \times E$  interactions across environments. It should be noted the transfer of cattle was only from the temperate (Montana) to a tropical (Florida) environment. Hence, the validity of the Rudder *et al.* (1986) results could not be tested in that experiment.

More recently, de Mattos *et al.* (2000) examined weaning weight records of  $\sim 3$  million Hereford calves across the United States, Canada and Uruguay. Genetic correlations across those environments all exceeded 0.85, indicating a general absence of genotype  $\times$  country interactions for weaning weight. Similarly, Jeyaruban *et al.* (2009) estimated  $G \times E$  interactions for growth, scanned carcass and reproductive traits in Angus cattle reared in Victoria (Mediterranean/temperate environments) or Queensland (warm temperate

environment) in Australia. Their results showed little evidence of  $G \times E$  for any of the traits across those environments.

Ibi *et al.* (2005) examined the effects of  $G \times E$  interactions on carcass quality attributes in Japanese Black cattle that originated in either Tohoku (20 106 animals born in a cold environment with large differences in temperature between summer and winter) or Kyusyu (34 670 animals born in a relatively warm climate throughout the year), with half of each cohort transferred to the alternate environment. A total of 54 776 carcass records were available for the study. Estimates of genetic correlations between the regions for the range of carcass traits were  $\geq 0.93$ . Corresponding estimates between management systems (reflecting length of feedlot finishing system) were all  $\geq 0.84$ . The authors concluded that  $G \times E$  interactions on carcass traits of Japanese Black cattle were biologically unimportant.

From these studies, it is concluded that  $G \times E$  within breeds may have a significant impact in poorly adapted breed types across extreme environments (tropical and temperate) or where breeding animals are selected in a stress-free environment for use in (sub)tropical environments. However,  $G \times E$  interactions are unlikely to be of major importance for *B. taurus* breeds across the temperate and relatively benign subtropical environments where they are traditionally grazed.

*Re-ranking of tropical breed sires across temperate and tropical environments.* This section examines the use of tropically adapted sires bred in the tropics and used to generate progeny that are raised in either temperate or tropical environments or under different management systems (e.g. pasture *v.* grain finishing).

Johnston *et al.* (2003a and 2003b) and Reverter *et al.* (2003a and 2003b) examined a wide range of live animal and carcass and beef quality attributes in Brahman, Santa Gertrudis and Belmont Red breeds in Australia to determine the impact of  $G \times E$  across: (a) tropical and temperate regions; (b) three market carcass weight end points (i.e.  $\sim 220$  kg,  $\sim 280$  kg or  $\sim 340$  kg); and (c) pasture- *v.* grain-finishing regimes. Estimates of genetic correlations showed little evidence of  $G \times E$  for any trait except P8 fat depth, meat colour and marbling in tropically adapted cattle across temperate- *v.* tropical-finishing environments and for retail beef yield and meat colour across feedlot *v.* pasture finishing. Genetic correlations for most measures of beef tenderness across markets and finishing regimes were close to unity except for cooking loss in a single muscle (*m. longissimus thoracis et lumborum*).

A subsequent major independent study based on Brahmans and Tropical Composites in northern Australia examined whether  $G \times E$  occurred for a wide range of productive and adaptive traits in steers managed in relatively benign environments from weaning at  $\sim 6$  months of age and fed a high grain diet over a 100-day finishing period relative to the performance of their half-sib heifers destined for the breeding herds and managed at pasture in (sub)tropical environments. Barwick *et al.* (2009a) found that in steers grown under commercial backgrounding and grain-finishing

environments,  $G \times E$  interactions were indicated by the presence of significant genotype  $\times$  cohort effects, with the mean cohort performance for a trait assumed to be the measure of environment level. Significant genotype  $\times$  cohort effects existed for many measures at and before the steers entered the feedlot, indicating the differences evident in Brahmans and Tropical Composites could change under different environmental conditions. There was a significant tendency for daily weight gains to increase more rapidly with improvement in environment in Tropical Composites than in Brahmans. The advantage in feedlot average daily gain in Tropical Composites is greater when conditions favour faster growth and less when growth conditions are poorer. The results emphasise the need for a population-specific understanding of trait relationships and of trait differences between measurement times in order to optimise breeding programme design.

Similarly, Wolcott *et al.* (2009) reported that genotype-specific evaluations will be necessary to accommodate different genetic relationships between meat quality, carcass and live animal traits. Brahmans and Tropical Composites were significantly different for some key meat quality and carcass traits, supporting the 'Meat Standards Australia' position that *B. indicus* content be included as a factor in meat quality grading (see papers in Thompson *et al.*, 2008). In addition, the developmental stage when live measurements were recorded and the production environment under which animals were managed at that age influenced the magnitude and, in some cases, the direction of genetic relationships between carcass and meat quality traits and live animal measurements. This emphasises the importance of thoroughly defining measurement protocols, including animal age and condition at time of assessment, for live animal traits that are to be included in a genetic evaluation analysis.

Barwick *et al.* (2009b) reported that Brahman heifers grew faster in wet seasons and slower in dry seasons than Tropical Composites, whereas Brahman steers grew slower than Tropical Composites throughout grow-out and finishing in different (sub)tropical and temperate feedlot environments. Brahman heifers were fatter and had higher condition scores at the end of wet and dry seasons than Tropical Composites, whereas Brahman steers had less fat and lower condition scores at the end of feedlot finishing. Numerous genetic correlations between heifers and steers differed substantially from unity, particularly in Brahmans, suggesting there may be scope to select differently in the sexes where that would aid their production roles (i.e. to improve reproduction and adaptation in females and feed efficiency and market attributes in steers).

The Barwick *et al.* (2009b) study also indicated that genetic correlations declined as measurement environments became more different, with the rates of decline sometimes differing between Brahmans and Tropical Composites. This occurred to varying extents for the traits and breeds examined, also suggesting the different breeds were sensitive to varying environments. For example, Brahman heifers seemed better able than the Tropical Composites to align

their growth with the feed available in 'wet' and 'dry' seasons and to retain fat up to the end of the 'dry' season. The re-ranking of Brahmans and Tropical Composites between heifers and steers for aspects of growth and fatness could represent a special case of  $G \times E$  (i.e. genotype  $\times$  sex interactions), given the confounding of sex and environment in the study.

There was, however, no evidence of re-ranking of sires for female reproductive performance across four different (sub)tropical environments (Johnston *et al.*, 2006). These results, together with results from selection experiments based on tropically adapted cattle in the tropics that suggest adaptive traits are genetically independent of productive traits (e.g. Burrow, 2001), indicate it is possible to effectively design optimal breeding programmes that use opportunities provided by  $G \times E$  across steer and heifer environments to maximise production and adaptation in beef cattle across both temperate and (sub)tropical environments.

Several other studies used data derived from national genetic evaluation schemes to evaluate  $G \times E$  interactions by distinguishing 'good' and 'poor' environments on the basis of mean performance levels of animals. Bradfield *et al.* (1997) used weaning weight records of 12 563 Santa Gertrudis calves to estimate (co)variance components. The analysis considered measurements on animals born in favourable Australian environments as Trait 1 and animals born in unfavourable production environments as Trait 2. An additive genetic correlation of 0.64 between production environments was significantly different from unity, suggesting the existence of genotype  $\times$  production environment interactions. However, when a sire  $\times$  contemporary group interaction effect was included in the model, the genetic correlation was not significantly different from unity, suggesting the ranking of Santa Gertrudis sires across production environments was caused by changes in ranking from one contemporary group to the next, rather than changes in ranking across production environments. This study clearly demonstrates the importance of including a sire  $\times$  contemporary group interaction when modelling  $G \times E$  interactions or undertaking genetic evaluations.

Similar findings were reported by Naser *et al.* (1996 and 1998) and Nephawe *et al.* (1999) in Bonsmara cattle in South Africa. Nephawe *et al.* (1999) examined the possible interactions between sire and four ecological regions using birth and weaning weight records of 43 628 calves from 18 herds. Genetic correlations and expected correlated responses to selection were estimated assuming the same trait to be a different trait when measured in each of the four different regions. The results indicate that for the purpose of genetic evaluation, the three Bushveld regions were the same, but the Highveld region could be considered as a separate environment, with selection of bulls bred on the Highveld for use in the Bushveld regions likely to be less effective than selection of bulls bred anywhere in the Bushveld and conversely. However, the results also confirmed that the interaction between sire and contemporary group was more important than between sire and any

designated region. The separate studies of Naser *et al.* (1996 and 1998) reinforce the importance of considering both permanent maternal environment and herd-year-season by sire interactions in evaluation of  $G \times E$  interactions. The authors concluded that excluding herd-year-season  $\times$  sire interaction could lead to a serious overestimation of the direct additive components of growth, with the same applying for permanent maternal environment, which if excluded could lead to a serious overestimation of maternal components of growth.

#### *Re-ranking of SNPs*

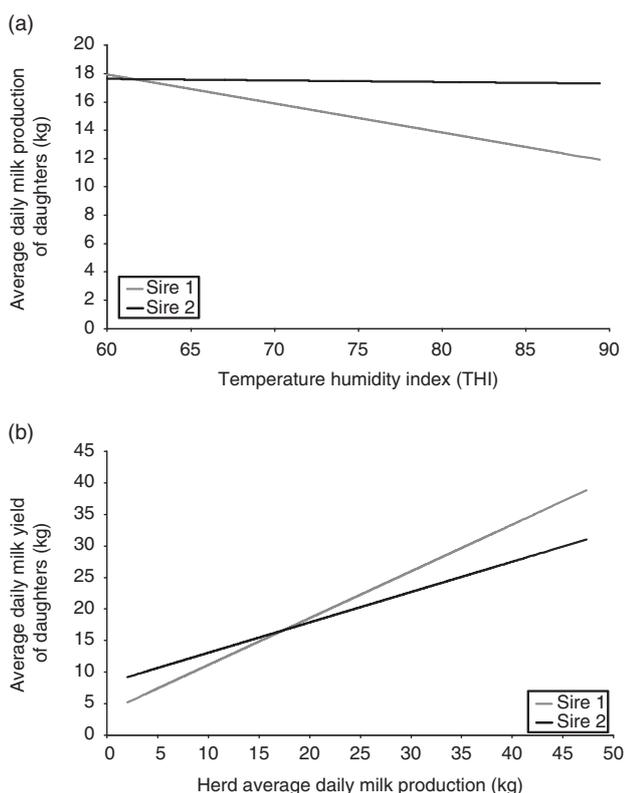
To date, there are no published reports on the extent of  $G \times E$  based on SNPs in beef cattle, although unpublished data from Australia, United States of America and Canada based on Illumina's BovineSNP50 Infinium Assay indicate significantly greater discord between significant SNP for growth, feed efficiency and carcass and beef quality attributes between Australia and North America relative to United States of America and Canada (Bennett GL, Goddard ME, Miller SP, Thallman RM *et al.*, unpublished results). These results were expected and they support published results from laboratory species, for example, reproductive performance in *Drosophila melanogaster* across three environmental treatments (Fry *et al.*, 1998) and broiler chicken mortality across commercial *v.* selection nucleus environments (Long *et al.*, 2008). Long *et al.* (2008) concluded there was unlikely to be a universally optimal SNP subset for predicting trait performance, although Fry *et al.* (1998) also reported there was no evidence for SNPs with opposite fitness effects in different environments.

It is possible that prediction equations based on genome-wide SNP associations (i.e. on tens of thousands of SNPs) may prove to be more reliable indicators of performance across environments than individual SNPs. This remains to be tested, at least in beef cattle.

In an Australian study in dairy cattle, Hayes *et al.* (2009) reported results from a genome-wide association study designed to detect SNPs associated with the sensitivity of milk production to environmental conditions (e.g. pasture rather than grain to feed cows and environments that differed substantially in daily ambient temperatures) across a wide range of production environments. Figure 2 shows the responses in milk production to environmental variables for the extreme sires under a varying temperature-humidity index and relative to performance as measured by herd average daily milk production, which was used as a surrogate for the level of feeding. SNPs associated with these responses to feeding level and temperature-humidity index were reported on chromosome 9 and 29, respectively, and were subsequently validated in two independent populations, one being a different breed of cattle. The authors suggested these validated marker panels could be used to select cows that are less sensitive to heat stress and low feeding level than average dairy cows.

In a separate study, Lillehammer *et al.* (2009) identified SNPs with significant effects for all milk production traits. The significant markers were categorised according to their joint effects on production and environmental sensitivity.

## Burrow



**Figure 2** Responses in milk production to environmental variables for different sires. (a) Predicted response in daily milk production of daughters to temperature humidity index for the two most extreme sires from the data set. (b) Predicted response in daily milk production of daughters to herd average daily milk production, a surrogate for the level of feeding, for two sires from the data set. Single nucleotide polymorphisms associated with these responses were validated on chromosomes 9 and 29 (Source: Hayes *et al.*, 2009).

Approximately one-third of the significant markers affected the intercept and slope in opposite directions, suggesting the possibility they could be used to facilitate marker-assisted selection for environmental sensitivity.

It is apparent that  $G \times E$  interactions will need to be considered in SNP association analysis of complex traits when undertaking genome-wide association studies, but the magnitude of their impact is still to be confirmed in well-designed livestock experiments.

### Strategies to maximise adaptation and production in different environments

On the basis of the several earlier reviews of the literature cited here, Burrow (2006) suggested a number of 'rules of thumb' that apply to optimally match 'genotypes' to their production and marketing environments and to overcome the detrimental impacts of  $G \times E$  interactions where they exist. These 'rules of thumb' as they apply to crossbreeding systems include:

1. Depending on the severity of the environment and the level of stressor challenge, 25% to 75% 'adapted genes'

are required for optimal production. Only exceptionally stressful environments require 100% 'adapted genes'.

2. 'Adapted genes' can be derived from *B. indicus* and their derivatives, as well as the tropically adapted taurine breeds. This provides an opportunity to take advantage of heterosis from crossbreeding and to maximise productivity without reducing resistance to environmental stressors below levels acceptable for the particular environment in which production is to occur.
3. For most (sub)tropical environments, optimal levels of productivity and adaptation will be achieved using a combination of multiple breed types (e.g. *B. indicus*, tropically adapted taurine, British, Continental).
4. In harsh (sub)tropical environments, some *B. indicus* content is required to ensure sufficient adaptation to parasites (mainly ticks and worms). The harsher and wetter the environment, the greater the need for *B. indicus* content.
5. Even in the harshest tropical environment, it is possible to combine *B. indicus* and adapted taurine breeds to optimise heterosis and maximise productivity. If 60% to 100% 'adapted genes' are required, a purebred tropically adapted taurine breed (e.g. Sanga or Criollo) could be combined with a *B. indicus* or *B. indicus*-derived breed to provide high levels of adaptation and capture the advantages of heterosis. If lower levels of adaptation (e.g. 25% to 60%) are required, an adapted taurine composite (e.g. Bonsmara, Senepol) could be combined with a *B. indicus* or *B. indicus*-derived breed to achieve desired levels of production and adaptation.

In breeds that are well adapted to their production environment, very few antagonistic relationships exist that would preclude simultaneous genetic improvement of both productive and adaptive traits through selection to maximise herd profitability in (sub)tropical environments. The major constraint to genetic improvement under commercial production systems in the (sub)tropics is the difficulty and expense of measuring the complete range of economically important productive and adaptive traits required to achieve a balanced breeding objective.

Genomic selection on the basis of SNPs offers new opportunities for commercial breeders to better breed and manage their cattle in future. However, to achieve the levels of accuracy of SNP-based prediction equations required by these breeders depends on the availability of very large cattle resource populations that have been accurately recorded for all economically important traits. Researchers are making very rapid progress in the development of high-density SNP panels, the cost of complete genome sequencing is dropping rapidly and the analytical methodology required to use these new technologies is also well under development. The major limitation for the next 5 to 10 years at least is likely to be the lack of large numbers of accurate phenotypes. This need has been recognised in several countries with specifically designed, industry-relevant programmes now being developed to generate these phenotypes in order to ensure that new growth opportunities for the beef industry can be captured.

## Acknowledgements

The findings from this review were presented at the 'Sustainable Animal Production in the Tropics: Farming in a Changing World' International Symposium held in Guadeloupe, 15–18 November 2010. Sincere thanks are due to INRA, BSAS, CIRAD, EAAP and WAAP for so generously funding the author's travel to participate in the symposium.

## References

- Barwick SA, Wolcott ML, Johnston DJ, Burrow HM and Sullivan MT 2009a. Genetics of steer daily and residual feed intake in two tropical beef genotypes and relationships among intake, body composition, growth and other post-weaning measures. *Animal Production Science* 49, 351–366.
- Barwick SA, Johnston DJ, Burrow HM, Holroyd RG, Fordyce G, Wolcott ML, Sim WD and Sullivan MT 2009b. Genetics of heifer performance in 'wet' and 'dry' seasons and their relationships with steer performance in two tropical beef genotypes. *Animal Production Science* 49, 367–382.
- Bradfield MJ, Graser H-U and Johnston DJ 1997. Investigation of genotype × production environment interaction for weaning weight in the Santa Gertrudis breed in Australia. *Australian Journal of Agricultural Research* 48, 1–5.
- Burns WC, Koger M, Butts WT, Pahnish OF and Blackwell RL 1979. Genotype by environment interaction in Hereford cattle: II. Birth and weaning traits. *Journal of Animal Science* 49, 403–409.
- Burrow HM 1997. Measurements of temperament and their relationships with performance traits of beef cattle. *Animal Breeding Abstracts* 65, 477–495.
- Burrow HM 2001. Variances and covariances between productive and adaptive traits and temperament in a composite breed of tropical beef cattle. *Livestock Production Science* 70, 213–233.
- Burrow HM 2006. Utilisation of diverse breed resources for tropical beef production. Proceedings of the 8th World Congress on Genetics Applied to Livestock Production, CD Rom, Communication No. 32-01, Organizing Committee WCGALP, Brazil, 8pp.
- Burrow HM and Dillon RD 1997. Relationships between temperament and growth in a feedlot and commercial carcass traits of *Bos indicus* crossbreds. *Australian Journal of Agricultural Research* 37, 407–411.
- Burrow HM and Prayaga KC 2004. Correlated responses in productive and adaptive traits and temperament following selection for growth and heat resistance in tropical beef cattle. *Livestock Production Science* 86, 143–161.
- Burrow HM, Seifert GW and Corbet NJ 1988. A new technique for measuring temperament in cattle. Proceedings of the Australian Society of Animal Production 17, 154–157.
- Burrow HM, Seifert GW and Hetzel DJS 1991. Consequences of selection for weaning weight in Zebu, *Bos taurus* and Zebu × *Bos taurus* cattle in the tropics. *Australian Journal of Agricultural Research* 42, 295–307.
- Burrow HM, Shorthose WR and Stark JL 1999. Relationships between temperament and carcass and meat quality attributes of tropical beef cattle. Proceedings of the Association for the Advancement of Animal Breeding and Genetics 13, 227–230.
- Burrow HM, Moore SS, Johnston DJ, Barendse W and Bindon BM 2001. Quantitative and molecular genetic influences on properties of beef. *Australian Journal of Experimental Agriculture* 41, 893–919.
- Burrow HM, Johnston DJ, Barwick SA, Holroyd RG, Barendse W, Thompson JM, Griffith GR and Sullivan M 2003. Relationships between carcass and beef quality and components of herd profitability in northern Australia. Proceedings of the Association for the Advancement of Animal Breeding and Genetics 15, 359–362.
- Davis GP 1993. Genetic parameters for tropical beef cattle in northern Australia: a review. *Australian Journal of Agricultural Research* 44, 179–198.
- de Castro JJ and Newson RM 1993. Host resistance in cattle tick control. *Parasitology Today* 9, 13–17.
- de Mattos D, Bertrand JK and Misztal I 2000. Investigation of genotype × environment interactions for weaning weight for Herefords in three countries. *Journal of Animal Science* 78, 2121–2126.
- Duarte-Ortuño A, Thorpe W and Tewolde A 1988. Reproductive performance of purebred and crossbred beef cattle in the tropics of Mexico. *Animal Production* 47, 11–20.
- Frisch JE 1981. Changes occurring in cattle as a consequence of selection for growth rate in a stressful environment. *Journal of Agricultural Science (Cambridge)* 96, 23–38.
- Frisch JE and Vercoe JE 1984. An analysis of growth of different cattle genotypes reared in different environments. *Journal of Agricultural Science (Cambridge)* 103, 137–153.
- Frisch JE and O'Neill CJ 1998. Comparative evaluation of beef cattle breeds of African, European and Indian origins. 2. Resistance to cattle ticks and gastrointestinal nematodes. *Animal Science* 67, 39–48.
- Fry JD, Nuzhdin SV, Pasyukova EG and Mackay TFC 1998. QTL mapping of genotype–environment interaction for fitness in *Drosophila melanogaster*. *Genetical Research*, Cambridge 71, 133–141.
- Hayes BJ, Bowman PJ, Chamberlain AJ, Savin K, van Tassell CP, Sonstegard TS and Goddard ME 2009. A validated genome wide association study to breed cattle adapted to an environment altered by climate change. *PLoS One* 4, e6676.
- Ibi T, Hirooka H, Kahi AK, Sasae Y and Sasaki Y 2005. Genotype × environment interaction effects on carcass traits in Japanese Black cattle. *Journal of Animal Science* 83, 1503–1510.
- Jeyaruban MG, Johnston DJ and Graser H-U 2009. Estimation of genotype × environment interactions for growth, fatness and reproductive traits in Australian Angus cattle. *Animal Production Science* 49, 1–8.
- Johnston DJ, Reverter A, Burrow HM, Oddy VH and Robinson DL 2003a. Genetic and phenotypic characterisation of live, carcass and meat quality traits from temperate and tropically adapted beef breeds. 1. Live animal measures. *Australian Journal of Agricultural Research* 54, 107–118.
- Johnston DJ, Reverter A, Ferguson DM, Thompson JM and Burrow HM 2003b. Genetic and phenotypic characterisation of live, carcass and meat quality traits from temperate and tropically adapted beef breeds. 3. Meat quality traits. *Australian Journal of Agricultural Research* 54, 135–147.
- Johnston DJ, Barwick SA, Holroyd RG, Fordyce G and Burrow HM 2006. Genetics of female reproduction traits. Proceedings of the Australian Beef – The Leader! Conference, March, pp. 47–52. Beef CRC, Armidale.
- Johnston DJ, Barwick SA, Fordyce G and Holroyd RG 2010. Understanding the genetics of lactation anoestrus in Brahman beef cattle to enhance genetic evaluation of female reproductive traits. Proceedings of the 9th World Congress on Genetics Applied to Animal Production. CD-Rom, Communication No. 0923, Organizing Committee WCGALP, Leipzig, Germany, 4pp.
- Johnston DJ, Barwick SA, Corbet NJ, Fordyce G, Holroyd RG, Williams PJ and Burrow HM 2009. Genetics of heifer puberty in two tropical beef genotypes in northern Australia and associations with heifer and steer production traits. *Animal Production Science* 49, 399–412.
- Kadel MJ, Johnston DJ, Burrow HM, Graser H-U and Ferguson DM 2006. Genetics of flight time and other measures of temperament and their value as selection criteria for improving meat quality traits in tropically adapted breeds of beef cattle. *Australian Journal of Agricultural Research* 57, 1029–1035.
- Kloosterman A, Parmentier HK and Ploeger HW 1992. Breeding cattle and sheep for resistance to gastrointestinal nematodes. *Parasitology Today* 8, 330–335.
- Koger M, Burns WC, Pahnish OF and Butts WT 1979. Genotype by environment interaction in Hereford cattle: I. Reproduction traits. *Journal of Animal Science* 49, 396–402.
- Koots KR, Gibson JP, Smith C and Wilton JW 1994. Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. *Animal Breeding Abstracts* 62, 309–338.
- Lillehammer M, Hayes BJ, Meuwissen THE and Goddard ME 2009. Gene by environment interactions for production traits in Australian dairy cattle. *Journal of Dairy Science* 92, 4008–4017.
- Long N, Gianola D, Rosa GJM, Weigel KA and Avendaño S 2008. Marker-assisted assessment of genotype by environment interaction: a case study of single nucleotide polymorphism–mortality association in broilers in two hygiene environments. *Journal of Animal Science* 86, 3358–3366.
- Mackinnon MJ, Meyer K and Hetzel DJS 1991. Genetic variation and covariation for growth, parasite resistance and heat tolerance in tropical cattle. *Livestock Production Science* 27, 105–122.
- Minjauw B and de Castro JJ 2000. Host resistance to ticks and tick-borne diseases: its role in integrated control. In 'Breeding for disease resistance in

- farm animals', 2nd edition (ed. RFE Axford, SC Bishop, FW Nicholas and JB Owen). CAB International Wallingford, UK.
- Montiel F and Ahuja C 2005. Body condition and suckling as factors influencing the duration of post partum anoestrus in cattle: a review. *Animal Reproduction Science* 85, 1–26.
- Morgan N and Tallard G 2007. Cattle and beef international commodity profile. Background paper for the Competitive Commercial Agriculture in Sub-Saharan Africa Study. Food and Agriculture Organisation of the United Nations.
- Murray M, Stear MJ, Trail JCM, d'Ieteran GD, Agyemang K and Dwinger RH 1991. Trypanosomiasis in cattle. Prospects for control. In 'Breeding for disease resistance in farm animals', 2nd edition (ed. RFE Axford, SC Bishop, FW Nicholas and JB Owen), pp. 203–223. CAB International Wallingford, UK.
- Nephawe KA, Naser FWC, Roux CZ, Theron HE, van der Westhuizen J and Erasmus GJ 1999. Sire  $\times$  ecological region interaction in Bonsmara cattle. *South African Journal of Animal Science* 29 (3), 189–201.
- Naser FWC, Konstantinov KV and Erasmus GJ 1996. The inclusion of herd-year-season by sire interaction in the estimation of genetic parameters in Bonsmara cattle. *South African Journal of Animal Science* 26, 75–78.
- Naser FWC, Erasmus GJ, van Wyk JB and Deventer CS 1998. Quantifying herd-year-season  $\times$  sire interaction in Bonsmara cattle. *South African Journal of Animal Science* 28, 167–172.
- Pahnish OF, Koger M, Urlick JJ, Burns WC, Butts WT and Richardson GV 1983. Genotype  $\times$  environment interaction in Hereford cattle: III. Post-weaning traits of heifers. *Journal of Animal Science* 56, 1039–1046.
- Pahnish OF, Urlick JJ, Burns WC, Butts WT, Koger M and Blackwell RL 1985. *Journal of Animal Science* 61, 1146–1153.
- Payne WJA and Hodges J 1997. Tropical cattle: origins, breeds and breeding policies. Blackwell Science, Oxford, London.
- Petherick JC, Holroyd RG, Doogan VJ and Venus BK 2002. Productivity, carcass and meat quality of lot-fed *Bos indicus* cross steers grouped according to temperament. *Australian Journal of Experimental Agriculture* 42, 389–398.
- Prayaga KC, Barendse W and Burrow HM 2006. Genetics of tropical adaptation in northern Australian cattle. Proceedings of the 8th World Congress on Genetics Applied to Livestock Production, CD Rom, Communication No. 16-01, Organizing Committee WCGALP, Brazil, 8 pp.
- Prayaga KC, Corbet NJ, Johnston DJ, Wolcott ML, Fordyce G and Burrow HM 2009. Genetic analyses of heifer adaptive traits and their relation to growth, pubertal and carcass traits in two tropical beef cattle genotypes. *Animal Production Science* 49, 413–425.
- Reverter A, Johnston DJ, Perry D, Goddard ME and Burrow HM 2003a. Genetic and phenotypic characterisation of live, carcass and meat quality traits from temperate and tropically adapted beef breeds. 2. Abattoir carcass traits. *Australian Journal of Agricultural Research* 54, 119–134.
- Reverter A, Johnston DJ, Ferguson DM, Perry D, Goddard ME, Burrow HM, Oddy VH, Thompson JM and Bindon BM 2003b. Genetic and phenotypic characterisation of live, carcass and meat quality traits from temperate and tropically adapted beef breeds. 4. Correlations among live animal, carcass and meat quality traits. *Australian Journal of Agricultural Research* 54, 149–158.
- Robinson DL and Oddy VH 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behavior of feedlot finished beef cattle. *Livestock Production Science* 90, 255–270.
- Rudder TH, Seifert GW and Burrow HM 1985. Environmental and genotype effects on fertility in a commercial beef herd in Central Queensland. *Australian Journal of Experimental Agriculture* 25, 489–496.
- Rudder TH, Seifert GW and Burrow HM 1986. Liveweights to 18 months of progeny sired by commercially bred and randomly selected bulls. Conference of the Australian Society of Animal Production 16, 347–350.
- Sorci G, Moller AP and Boulinier T 1997. Genetics of host-parasite interactions. *Trends in Ecology and Evolution* 12, 196–200.
- Stear MJ and Murray M 1994. Genetic resistance to parasitic disease: particularly of resistance in ruminants to gastrointestinal nematodes. *Veterinary Parasitology* 54, 161–176.
- Stear MJ, Bishop SC, Mallard BA and Raadsma H 2001. The sustainability, feasibility and desirability of breeding livestock for disease resistance. *Research in Veterinary Science* 71, 1–7.
- Stear MJ, Hetzel DJS, Brown SC, Gershwin LJ, Mackinnon MJ and Nicholas FW 1990. The relationships among ecto- and endoparasite levels, class I antigens of the bovine major histocompatibility system, immunoglobulin E levels and weight gain. *Veterinary Parasitology* 34, 303–321.
- Stein J, Ayalew W, Rege JEO, Mulatu W, Malmfors B, Dessie T and Philipsson J 2009. Livestock keeper perceptions of four indigenous cattle breeds in tsetse infested areas of Ethiopia. *Tropical Animal Health and Production* 41, 1335–1346.
- Thompson JM, Polkinghorne R, Anderson CA and Webb LE 2008 (eds) Meat standards Australia. A Special Edition of the Australian Journal of Experimental Agriculture 48 (11), 129.
- Turner HG 1982. Genetic variation of rectal temperature in cows and its relationship to fertility. *Animal Production* 35, 401–412.
- Turner HG 1984. Variation in rectal temperature in a tropical environment and its relation to growth rate. *Animal Production* 38, 417–427.
- Turner HG and Short AJ 1972. Effects of field infestations of gastrointestinal helminths and of the cattle tick (*Boophilus microplus*) on growth of three breeds of cattle. *Australian Journal of Agricultural Research* 33, 177–193.
- Wolcott ML, Johnston DJ, Barwick SA, Iker CL, Thompson JM and Burrow HM 2009. The genetics of meat quality and carcass traits in two tropical beef genotypes and the impact of tenderstretch on genetic and phenotypic tenderness. *Animal Production Science* 49, 383–398.
- World Bank 2009. 'Minding the stock: bringing public policy to bear on livestock sector development' Report No. 44010-GLB. The World Bank, Washington DC, USA. Papers are available as open access manuscripts through CSIRO Publishing at <http://www.publish.csiro.au/nid/17.htm>
- Papers are available as open access manuscripts through the Livestock Library at <http://www.livestocklibrary.com.au>