

SYNTHESIS

Evolutionary process of *Bos taurus* cattle in favourable versus unfavourable environments and its implications for genetic selection

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adaptation, breeding, cattle, environment, genetic improvement, trait.

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Abstract

The evolutionary processes that have enabled *Bos taurus* cattle to establish around the globe are at the core to the future success of livestock production. Our study focuses on the history of cattle domestication including the last 60 years of *B. taurus* breeding programmes in both favourable and unfavourable environments and its consequences on evolution and fitness of cattle. We discuss the emergence of 'production diseases' in temperate production systems and consider the evolutionary genetics of tropical adaptation in cattle and conclude that the Senepol, N'Dama, Adaptaur and Criollo breeds, among others with similar evolutionary trajectories, would possess genes capable of improving the productivity of cattle in challenging environments. Using our own experimental evidence from northern Australia, we review the evolution of the Adaptaur cattle breed which has become resistant to cattle tick. We emphasize that the knowledge of interactions between genotype, environment and management in the livestock systems will be required to generate genotypes for efficient livestock production that are both economically and environmentally sustainable. Livestock producers in the 21st century will have less reliance on infrastructure and veterinary products to alleviate environmental stress and more on the animal's ability to achieve fitness in a given production environment.

Introduction

Whilst both natural evolutionary processes and modern genetic selection result in phenotypic changes, the mechanisms that determine the changes are quite different. Evolution is dynamic natural change in response to environmental pressure. Genetic selection is artificial directed change largely independent of environmental pressure. Within modern agriculture, genetic selection has been able to maximize directed change by minimizing environmental pressures. The environmental pressures are managed through intervention strategies such as providing high quality feeds, artificial housing or drugs to restrict disease. These intervention strategies are energy dense and enable agriculture to maximize outputs (productivism); however, they result in populations that are unable to withstand the pressure of more 'natural' environments. In some cases, the extreme selection for a single trait can result in physiological breakdown as resources are chan-

nelled towards particular production proteins. This study explores how evolutionary genetics might help inform modern cattle breeding programmes and shows some examples from tropically adapted cattle. We consider the importance of environmental stress for identifying robust genotypes in production systems that will increasingly need to focus on efficiency rather than total productivity.

Since the 1950s in the developed countries, the era of agricultural productivism emerged with a corresponding demise in the influence of natural selection in livestock production systems. Livestock productivism was characterized by a significant use of technology, both mechanization and biotechnology, to maximize productive output. This productivism was facilitated by relatively abundant cheap fossil fuels; environmental regulation removed environmental stressors to allow intensification, concentration and specialization of the systems (Ilbery and Bowler 1998). The genetic diversity of both *Bos taurus* and *Bos indicus* cattle was reduced with the concen-

tration on breeds and sires within breeds that had the highest production potential. More recently, there has been a trend for a measured increase in productivity and growing pressure for cattle production systems to manage their total carbon budgets, which will require a reduction in their greenhouse gas emissions. The reduction in the use of fossil fuel derived energy and nutrients (direct: fuel and fertilizer; indirect: acaricide, anthelmintics and vaccine) will reduce the ability to manage directly environmental stress. A paradigm shift in priorities is therefore required – more diverse genotypes that are productive in a range of environments will need to be developed. The evolutionary path of cattle since domestication provides insight into the current fitness levels as well as a better understanding of the interactions between cattle genotypes, environments and management intervention strategies (hence forth called $G \times E \times M$ interactions).

There has been a long history of domestication and implicit genetic selection; however, systematic breeding programmes have only been used over the last 60 years. These breeding programmes have enabled cattle to meet specific roles: predominantly supplying meat and milk for human consumption. There are hundreds of distinct cattle breeds around the world. However, a recent article published in *Science* (The Bovine HapMap Consortium 2009) looked at the process of cattle domestication. Their analyses (based on mutation rate, inbreeding rate, linkage disequilibrium levels, etc.) revealed that cattle have undergone a rapid recent decrease in effective population size from a very large ancestral population, possibly due to bottlenecks associated with domestication, selection and breed formation. This study also provided genetic relatedness amongst these breeds. Hence, any future proposal for evolutionary management of cattle domestication should consider this worldwide structure of the breeds to design conservation programmes and mating schemes. The reduction in the ancestral population diversity has important implications for breeding programmes in the 21st century.

The opportunity for modern cattle breeds to evolve in response to environmental stress is restricted as the diversity of the gene pool of cattle populations diminishes. However, there are examples of cattle breeds that have demonstrated rapid evolutionary change: in particular where *B. taurus* cattle have been reared in challenging tropical environments. The Adaptaur of northern Australia is a European *B. taurus* (interbred Hereford–Shorthorn) that has undergone a relatively rapid transition from extreme susceptibility to extreme resistance to cattle tick via a synergy between natural and artificial selection for tick resistance (Frisch 1981; Hetzel et al. 1990; Frisch et al. 2000). The evolution of the Adaptaur under tropical

stress provides a model approach to cattle breeding, which, if applied within the broader livestock industries might determine more favourable genotypes especially in the advent of escalating environmental stress due to climate change.

This study explores the consequences of selection for production traits and demonstrates evolutionary genetics of taurine cattle in both temperate (favourable) and tropical (unfavourable) environments. As an example of evolutionary adaptation we focus on the Adaptaur from northern Australia; however, we also draw on examples from three other *B. taurus* breeds that all have evolutionary backgrounds in unfavourable environments: Senepol from the Caribbean, the Criollo breed group from Central and South America and the N'Dama from West Africa. We show how exposure to a specific environmental stress (cattle tick infestation in a tropical environment) demonstrates the potential for experimental evolution to generate new more robust genotypes that can perform in environmentally stressful environments. Genetic adaptation of cattle for a successful transition into the postproductivism era must incorporate alleles of economic importance from genotypes adapted to potentially more stressful environments. The principles of evolutionary genetics can be used to facilitate Darwinian fitness in future livestock breeding programmes to generate optimal genotypes for a low-cost and environmentally sustainable production system. In essence, there are complex interactions between genotype, environment and management ($G \times E \times M$) in the livestock systems and the implications relate to: (i) fitting the right genotypes to the right environments and production systems and (ii) determining the optimal genotype across a range of environments and production systems. We provide some perspectives on $G \times E \times M$ and how this could contribute to evolution of future strains or breeds of cattle.

Historical movement of African and European *Bos taurus*

About 10 000 years BP (before present), Neolithic hunter-gathers began to domesticate simultaneously both *B. taurus* (Fertile Crescent and Saharan Africa) and *B. indicus* (Indian subcontinent) (Bradley et al. 1998; Bruford et al. 2003; Chen et al. 2010). The history of *B. indicus* in Asia (Harris 1992), and more recent introduction to Africa via the African east coast about 3500 years BP (Hanotte et al. 2002), is notable for the high levels of environmental stress associated with indicine evolution. The heterosis achieved from *B. taurus* \times *B. indicus* crossbreeding is well documented (e.g. McDowell et al. 1996). However, some African taurine breeds, such as N'Dama, were able to survive in stressful tropical environments with little or no

B. indicus hybridization¹ (Frisch et al. 1997; Anderung et al. 2007).

In Europe, *B. taurus* accompanied Neolithic Man's conversion from nomadic hunter-gatherer to a sedentary agriculturalist and cattle evolved adaptations to temperate climates. Under various Celtic, Germanic and Nordic tribes, there was a general divergence of the larger continental breeds (e.g. Charolais, Simmental) from the medium-sized British breeds (e.g. Hereford, Red Poll, Murray Grey) and specialization into dairy (e.g. Holstein, Jersey), beef (e.g. Angus, Shorthorn) and dual purpose (e.g. Brown Swiss). In the developed regions of Europe, cattle increased their propensity to supply meat and milk through increased industrialization and dedicated breeding programmes.

European taurine cattle were also subjected to the stressors of tropical and semi-arid regions as these cattle were a significant component of the human colonization of Central and South America by the Spanish and Portuguese during the 16th century. Cattle from the colonization were collectively known as Creole or Criollo,² and adapted to the environments that ranged from semi-arid to the wet tropics (Russell et al. 2000; Mariante et al. 2009). Also regarded as tropically adapted is the Senepol, a two-breed composite of N'Dama and Red Poll cattle, bred on the Caribbean island of St Croix in 1918 (Hammond et al. 1996). Moreover, northern Australia witnessed the formation of tropically adapted taurine composites. Herefords and Shorthorns, first imported into Australia from United Kingdom in 1826, along with the South African cattle breed, Africander imported from *King Ranch*, Texas, USA in 1953 formed part of a CSIRO research programme at the *Belmont* Research Station, Rockhampton in the 1950s (Kennedy and Turner 1959). Selection lines within a four-breed composite of Africander, Brahman, Hereford and Shorthorn, commercialized as Belmont Red, and a two-breed composite of Hereford and Shorthorn (HS line) were established. The HS line was partially commercialized as Adaptaur in 1985 (O'Neill et al. 1998).

***Bos taurus* breeding programmes in favourable environments – productivism and its consequences**

Modern genetic selection programmes are capable of delivering cumulative gains of 1–2% per annum for the

¹African *indicine* and *taurine* crossbred cattle are generally referred to as Sanga cattle.

²Creole or Criollo – Spanish words referring to descendants of Iberian livestock transported to Central and South America during colonization of these countries by the Spanish and Portuguese.

trait (or combination of traits) under selection (Simm et al. 2000). Quantitative genetic methods have been a crucial component of productivism: development of selection index principles in animal breeding programmes in early 1940s (Hazel and Lush 1943) followed by application of Best Linear Unbiased Prediction (BLUP) of animal's genetic merit from early 1970s: the animal model (Henderson 1975). These methods accurately quantify breeding potential (estimated breeding values or EBVs; expected progeny differences or EPDs) for economically important traits and are expressed in real units of measurement (e.g. kg for growth rate). To assess the relative superiority of a bull or a cow, the animal's EBV is compared with those reported by a breed average. With continuing advances in statistical and computing technology, quantitative geneticists successfully refined and modified BLUP methodology as new performance records (e.g. on daily growth) and associated new traits became available. Utilizing these sophisticated levels of technologies, livestock industries of the developed countries have achieved significant increases in the product quantity and quality within the optimal (i.e. stress-free) environments (Rauw et al. 1998; Bishop and Woolliams 2004; Maas et al. 2009). High performance under these stress-free environments does not, however, imply high performance in all environments. Whilst quantitative genetic techniques have successfully identified superior performing individuals and selectively bred from them, the selection process has been largely under increasingly optimal environments (i.e. stress-free). There is an emerging question of the costs of 'stress-free selection' as genotypes are exposed to more stressful environments. Whilst management intervention has increasingly reduced environmental stress the ability for an individual to respond has decreased as genetic selection has refined metabolic pathways towards product output at the expense of other traits such as disease resistance.

For the dairy industries the concern has been the emergence of 'production diseases' (e.g. lameness and metabolic and reproductive disorders), in parallel with increasing levels of milk production (Lucy 2001; Mulligan and Doherty 2008; Ward 2009). However, research and breeding programmes of dairy cattle have started to shift emphasis from production-only traits in the breeding goal to traits that are associated with robustness (e.g. resistance to clinical mastitis, lameness and milk fever) and sustainability (e.g. fertility, feed efficiency, conformation, optimal behaviour) (Distl 2000; Kadarmideen et al. 2000; Kadarmideen and Pryce 2001; Neuenschwander et al. 2005). Beef cattle breed societies have gone down a similar path to the dairy industries with the emphasis on performance recording production traits. In beef cattle breeding, growth, calving ease, reproduction and meat

quality traits such as muscle and/or fat depth and tenderness are the main drivers of commercial operations. As with the dairy industries there has been an increase in persistent production diseases in the beef industries; namely respiratory diseases and metabolic disorders in the feedlot systems (e.g. Owens et al. 1998; Garcia et al. 2010). Continuing outbreaks of the ocular disease called infectious bovine keratoconjunctivitis (IBK) also generates significant economic and welfare issues for the cattle industries (Brown et al. 1998; Snowden et al. 2005). These problems have been addressed through research to develop animal management protocols, feed additives, pharmacological agents and vaccines to combat the diseases (Quigley et al. 1997; Galyean and Rivera 2003; McConnel et al. 2007; Carriquiry et al. 2009; Marcillac-Emberson et al. 2009) and demonstrates a classic 'environment control' strategy. However, genetic methods for the identification of host resistance/susceptibility for diseases such as IBK in the US Department of Agriculture reference cattle population (Casas and Stone 2006) and Australian Adaptaur cattle (Ali et al. 2010) are being explored.

The animal model can be used to evaluate genetic merit of animals for traits associated with the production diseases described above (Heringstad et al. 2000; Kadarmideen et al. 2000). It is not only possible to select animals for just one trait, but rather a combination of traits. Hence, animals' EBVs for different traits (e.g. growth, reproductive success and some measures of adaptability like IBK resistance) are combined to form an aggregate or total breeding value (TBV). Therefore, a multi-trait breeding objective would appear as:

$$\hat{A} = b_1EBV_1 + b_2EBV_2 + \dots + b_nEBV_n,$$

where \hat{A} is the total breeding value, b_i is an economic weight for the i th trait in breeding objective, EBV_i is the EBV for the i th trait and n is the number of traits in the breeding goal. Breeders can modify their herd's genetics based on assigning different economic weights to different traits; for instance if adaptability or disease resistance is more important than other traits in tropical environments, then there needs to be higher weights for those traits in the breeding goal. Application of these novel methods has had major beneficial effects on the cost and quality of food, and on the efficiency, competitiveness and welfare status of the livestock industries concerned. The incorporation of resistance traits ensures that the TBV is also driven by evolutionary principles of adaptation.

However, in any breeding programme the animal's physiological limits must be considered. In production systems of negligible environmental stress, the need for

both energy and physiological mechanisms to alleviate stress are not required. In theory, the metabolic energy is therefore available for production traits but with continued selection for high production the dairy cow is unable to consume enough energy to meet this production potential and the cow's fertility (Butler and Smith 1989; Kadarmideen et al. 2003; Wathes et al. 2009) and health (Ingvarsen et al. 2003; Zuerner et al. 2007; Mulligan and Doherty 2008) suffer as a consequence. Moreover, a number of studies have shown a negative relationship between metabolic rate and resistance to stress (see Parsons 1990 and Hoffmann and Parsons 1991). Animals of low resistance to environmental stress have inherently higher rates of growth, appetite and fasting metabolism than animals relatively resistant to environmental stress (Frisch and Vercoe 1984). Thus, selection for production traits, disregarding physiological limits, fertility and resistance to environmental stress, would have serious negative consequences for future cattle herds as cows can only be maintained with high inputs that are unsustainable in the longer term.

The three main genetic processes involved in the evolution of animals during domestication are selection, genetic drift and inbreeding (Falconer and Mackay 1996), and inbreeding is posing additional problems for the intensive cattle industries. Inbreeding can lead to loss of fitness and even survival of a breed or species. For the dairy industry in the USA, Smith et al. (1998) found that the effects of inbreeding in the Holstein herd, years 1983–1993, were cumulative and larger on lifetime profit functions than on lactation traits. Techniques are now available to control inbreeding using conventional BLUP methods (Villanueva et al. 2006) or using molecular genetic markers in genetic improvement programmes (e.g. Li et al. 2008). Hence, any future breeding programmes must be designed to manage inbreeding depression (Kearney et al. 2004; Fernández et al. 2008).

In recent decades, cattle breeds of the developed countries have been subjected to breeding programmes that are not sustainable and inappropriate for determining genotypes that are productive in unfavourable environments. Stern and Orgogozo (2009) suggest that there is a need to identify and select specific mutations without negative consequences. We argue that for cattle of the 21st century it will be necessary to also explore the evolution of cattle in unfavourable environments, where there has been selection for alleles at many loci offering specific environmental adaptations. The next section provides some examples of breeding programmes that have identified desirable genetics contributing to adaptations of temperate cattle breeds to unfavourable tropical environments.

***Bos taurus* breeding programmes in unfavourable environments: tick resistance and tropical adaptation**

Modern agricultural populations of plants and animals have shown rapid evolutionary adaptation to environmental stress in timeframes of decades (or less) (Thompson 1998; Bell and Collins 2008; Campbell et al. 2009). Environmental stress is defined as an environmental force, from either biotic or abiotic factors, that impairs an animal's regulatory mechanism to such an extent that fitness is compromised. Fitness, an animal's ability to grow and reproduce viable offspring will be adversely affected if the animal is unable to mount an appropriate response to the stressor via means of its physiology and/or behaviour. The degree of sensitivity to these stressors, or homeostasis, will be regarded as an aspect of fitness (Falconer and Mackay 1996). In a relatively short period of time, European *B. taurus* relocated from temperate to tropical regions and had to achieve higher fitness in the presence of tropical stressors. This higher fitness was achieved through the application of evolutionary principles within a genetic selection program.

The response to environmental stress involves a synergy between behaviour and physiological adaptation (Hart 1990; Hoffmann and Parsons 1991; Lomborg et al. 2008). Documenting the plethora of tropical environmental stressors and the corresponding responses of *B. taurus* to these stressors is beyond the scope of this study. Therefore, we present data from experiments that aimed to assess the evolutionary adaptation of *B. taurus* cattle to stress from infestations of the ectoparasite cattle tick *Rhipicephalus (Boophilus) microplus*. Cattle tick infestations have a substantial negative impact on host fitness (Frisch and Vercoe 1984; Lehmann 1993). By the end of last century, estimates of the yearly global costs of cattle tick and tick-borne diseases were between US\$13.9 and US\$18.7 billion (de Castro 1997). The global costs of ticks are set to escalate; increasing levels of acaricide resistance (Sangster 2001), limited efficacy of anti-tick vaccines and emergence of nonresponders to vaccination (Outteridge 1993; Sonenshine et al. 2006), the genetic antagonism on fitness traits from biased artificial selection for production traits (Frisch 1981; Kadarmideen et al. 2000) and the potential negative impact of climate change (White et al. 2003). Exploring the full repertoire of the animal's anti-tick mechanisms is warranted if genetic technologies that utilize naturally occurring adaptation to parasitic stress are going to contribute to sustainable livestock production.

European taurine cattle, such as the Criollo in the 1500s, were relocated to their respective tropical environments from temperate environments that were free of

parasites endemic in the tropics. A similar case occurred in 1952 with the introduction of Herefords and Shorthorns (HS line) on the CSIRO *Belmont* Research Station, a property located 26 km NNW of Rockhampton, in north-eastern Australia. As a research station located in the tropics, acaricide was initially used routinely to treat tick infestations but from 1966 it was used only as an experimental treatment or to prevent mortalities from tick infestations (Frisch 1981). Thus on *Belmont*, there was a need to select European *B. taurus* cattle which had anti-parasitic mechanisms to enable them to survive and maintain fitness. Cattle, as with other herbivores, have evolved various anti-tick mechanisms: multiple immunological processors, hypersensitivity and exudate and grooming behaviour (Riek 1962; Roberts 1968a; Schleger et al. 1981; Brossard and Wikel 2004). Roberts (1968b) also showed that rejection of larvae on *B. taurus* occurred within 24 h of infestation and the effect was greater in animals resistant to tick. As pointed out by Roberts (1968b) the early mortality of larvae has implications for the restricted transmission of such tick-borne diseases as *Babesia bigemina*. A family within the HS line on *Belmont* did acquire extreme resistance to infestations of cattle tick (Frisch et al. 2000).

The origins of the Adaptaur began on *Belmont* in 1980 with the identification of a heifer (animal identity: 790546) of the 1979 calf crop of the HS line and after 1980 selection for both high growth tick resistance within the HS line focused on this family. The heifer acquired extreme resistance to field infestations of cattle tick soon after weaning (subsequent counts of zero or one regardless of tick counts of cohorts – see Fig. 1 for tick counts of cohorts). There was no evidence of hypersensitivity (J. E. Frisch and C. J. O'Neill, unpublished data) and a grooming response to remove larvae within 24 h of infestation (C. J. O'Neill and J. E. Frisch, unpublished data). Figure 1 presents a compilation of tick count data from various studies of the 1980s on adaptation, production or heterosis [see Frisch and Vercoe (1984), Frisch (1987), Frisch et al. (2000) for details of environment, breeding programmes experimental designs and various analyses of data]. These studies were conducted as a precursor to a major heterosis study conducted during the 1990s, involving breeds of European, Indian and African origins, to identify the optimal genotype for herd productivity in a stressful tropical environment (Frisch and O'Neill 1998a,b,c). Figure 1 illustrates that there is a strong tendency in low tick counts of progeny from sires of the 790546 family compared to progeny from sires of the remaining Adaptaur herd and progeny from the Brahman sires. The focus on the maternal lineage of 790546 not only assisted in rapid reduction in the phenotypic trend in tick count (Fig. 1), but also a corresponding linear

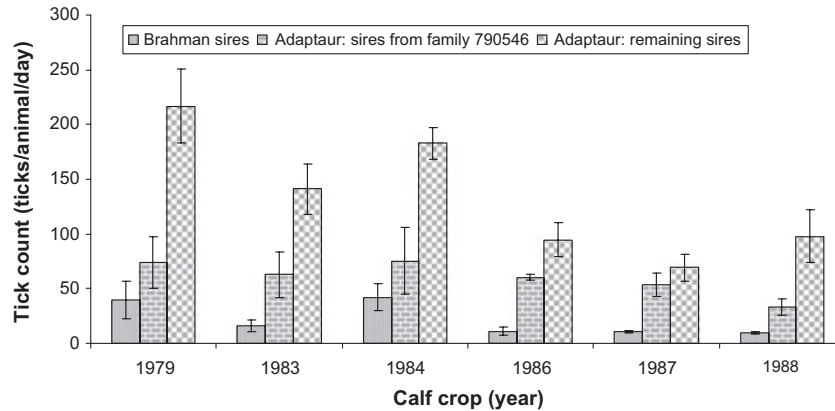


Figure 1 Arithmetic means (three highest counts for the calf crop) (\pm SEM) of field tick (*Rhipicephalus microplus*) infestations of heifer progeny of Brahman and Adaptaur sires for calf crops 1979, 1983–1984 and 1986–1988 on Belmont Research Station. Number of sires and progeny per group: Brahman, 24 sires with 159 progeny, Adaptaur maternal lineage 790546, five sires with 55 progeny, and remaining Adaptaur, 20 sires with 109 progeny.

($R^2 = 0.93$) genetic trend from 1983 to 1998 of a mean rate of 7 ticks/year of the Adaptaur herd (Frisch et al. 2000). A similar genetic trend was found by Henshall (2004).

Twenty-seven years after the identification of heifer 790546, in 2007 descendents from this heifer exhibited high tick resistance (Table 1) and with some straightbred animals (e.g. animal identities: 060017 and 060031) resembling the extreme phenotype of 790546 (Table 2). Tick count data from an experiment conducted on Belmont during November and December 2007, involving 2-year-old heifers are presented in Tables 1 and 2. This experiment was aimed at studying tick resistance of different breed types and observing host hypersensitivity to tick larvae. Animals were sourced for this experiment as follows: there were 15 Brahman heifers chosen at random from a calf crop of 140 heifers from Belmont Research Station and the Adaptaur and Adaptaur cross-breds were sourced locally from commercial Seedstock producers *Vineree* and *Ben M'Cree*. To restrict the immediate host grooming to remove tick larvae, we fitted a collar to the animal and taped a tube of larvae onto the collar. These cattle were artificially infested with 10 000 two-week-old tick larvae (*R. microplus*, Queensland Department of Primary Industries and Fisheries, Yeerongpilly, Australia). At 48-h postinfestation, all heifers were assessed for their degree of hypersensitivity. The Adaptaur straightbred has not lost its high resistance to cattle tick, even after 27 years (Table 1), and this high tick resistance appears to be conferred to other taurine breeds regardless of their genetic background for tick resistance (Table 2). The finding that some heifers with high counts at 6 months of age have progressively lower counts at 12 months of age and 24 months of

Table 1. Number of *Bos indicus* (straightbred Brahman) and *Bos taurus* (Adaptaur and F₁ Adaptaur cross) 24-month-old heifers in each class of tick resistance from an artificial infestation of cattle tick (*Rhipicephalus microplus*) on Belmont Research Station November 2007*.

Tick resistance class (cumulative tick count)†	Number of heifers in tick class		
	Brahman	Adaptaur	Adaptaur F ₁
Very low (>150)	0	0	0
Low (81–150)	0	0	0
Average (31–80)	3	1	0
High (11–30)	4	0	1
Very high (1–10)	8	3	2
Extreme (0)	0	4	3
Daily weight gain (kg/day) during the tick infestation experiment	1.03 \pm 0.048	1.08 \pm 0.066	1.13 \pm 0.077

*To confirm the viability of the tick larvae a straightbred Murray Grey heifer from *Ben M'Cree* of known high susceptibility (field counts >100 ticks/side at both 6 and 12 months of age at *Ben M'Cree*, personal communication P and L Quayle) of the same cohort was pastured with the above heifers at Belmont and produced a count of 233 mature ticks by day 21 of the artificial infestation.

†Tick resistance class was based on number of maturing ticks from cumulative tick counts (/side) on days 19–21 from an artificial infestation of 10 000 larvae.

age (Table 2) confirms that resistance is acquired. Although general hypersensitivity was not observed in this experiment, five of the most tick resistant *B. taurus* heifers had a small area (approx. 5 cm in diameter) of exudate ranging from minor to excessive at the site of larval release (Table 2), indicating a host immune response to the parasite. By day 15, there was no evidence of exudate. The relatively high weight gain on pasture of the Adap-

Table 2. *Bos taurus* (Adaptaur straightbred and F₁ Adaptaur cross) heifers with individual tick counts (*Rhipicephalus microplus*) at 6, 12 and 24 months of age and an assessment of the degree of exudate at the site of larval release from an artificial infestation of cattle tick at 24 months of age on Belmont Research Station, November 2007.

Genotype	Animal identity	Sire breed	Dam breed	Tick count at age (months)			Exudate‡
				6*	12*	24†	
F ₁ Adaptaur cross	060001	Simmental	Adaptaur	>100	>100	24	Nil
	060021	Simmental	Adaptaur	>100	67	7	Nil
	060064	Tuli	Adaptaur	>100	8	7	Nil
	060006	Simmental	Adaptaur	25	9	0	Nil
	060037	Adaptaur	Murray Grey	10	23	0	Moderate
	060003	Senepol	Adaptaur	0	0	0	Excessive
Adaptaur straightbred	060044	Adaptaur	Adaptaur	>100	17	2	Nil
	060042	Adaptaur	Adaptaur	>100	17	0	Nil
	060037	Adaptaur	Adaptaur	26	3	2	Minor
	060017	Adaptaur	Adaptaur	1	4	0	Excessive
	060031	Adaptaur	Adaptaur	1	2	0	Excessive

*Tick counts (/side) courtesy of P and L Quayle from field infestations at *Ben M'Cree*, Peachester, Queensland, Australia.

†Cumulative tick counts (/side) on days 19–21 from the artificial infestation of 10 000 larvae.

‡Exudate assessed at the site of larval release 48-h postinfestation of the 10 000 larvae.

taur straightbred and F₁ compared to the Brahman (Table 1) would suggest that neither the imposition of 10 000 tick larvae nor the Adaptaur anti-tick mechanism was detrimental to their productivity. The results presented in Tables 1 and 2 suggest a relative advantage of Adaptaur and Adaptaur cross-over Brahmans in tick resistance at the same level of growth. However, if strong conclusions are to be made, a larger sample size in each of the breed classes would be required and a statistical analysis conducted.

Evolutionary genetics of adaptation to environmental stressors in the tropics

Just as the African *B. taurus* evolved mechanisms for resistance to tropical stress so did the European *B. taurus*. There are a number of adaptation mechanisms that could explain the relatively high levels of resistance to tropical stressors for the Adaptaur, N'Dama, Senepol and Criollo breeds. The following scenarios highlight the complexity of disease resistance and pertain to evolutionary genetics: chance mutations, a synergy between natural selection and artificial selection and phenotypic plasticity. Moreover, adding to this complexity Colditz (2002) and Viney et al. (2005) contend that the host's optimum immune response to parasites and pathogens is one of immunosufficiency, because the former is a balance between energy loss due to pathogen infection and energy expenditure mounting an immune response that is conducive to fitness. Naessens (2006) has shown that it is the inappropriate response of the immune system that results in the mortality and morbidity of trypanosome-

infected cattle. N'Dama not only possesses a genetic capacity to control parasitism (Claxton and Leperre 1991), but also to avoid anaemia and the severe pathology associated with trypanosome infection (Murray and Dexter 1988; Naessens 2006). A major gene for hair length 'slick hair' that contributes to improving the animal's thermoregulatory ability, has been described in both Senepol and Venezuelan Carora – a two-breed composite of Brown Swiss and local Criollo (Olson et al. 2003). It could be speculated that the Senepol also has the potential for high tick resistance given its N'Dama origin and slick coat (Claxton and Leperre 1991; Hammond et al. 1996). O'Kelly and Spiers (1983) using animals from the HS line, among other breeds, demonstrated that fewer ticks matured on clipped areas of coat compared to unclipped areas.

Relative to their temperate origins, the environmental assault on the HS line on Belmont was extreme, from solar radiation, heat stress, parasites and periods of poor nutrition, thus creating strong natural selection. A live-stock population surviving with minimal intervention to remove environmental stress, such as not treating the Adaptaur with acaricide to remove parasites, means that the population was under natural selection pressure. Using both calf survival data and a multi-trait mixed model genetic analysis of growth rates from 1966 to 1981, Hetzel et al. (1990) concluded that the fitness of this population was increasing under natural selection. Moreover, with the artificial selection protocol in place, selecting sires for high growth rate in a stressful environment (Frisch 1981), was working in synergy with natural selection (Hetzel et al. 1990). Frisch (1981) also concluded that the

increasing level of resistance to environmental stress was solely responsible for the improved growth rates for this population. Since 1983, the additional selection protocol of high tick resistance focusing on a single family with selection for high growth rate, confirmed the value of targeting components that positively impact on productivity in a stressful tropical environment. The 33% improvement in calving rates of Adaptaur cows from 1992 to 1996, compared to Adaptaur before selection 1964–1972 (O'Neill and Frisch 1998), is further evidence that high selection intensity (high growth and high tick resistance) on fitness traits was successful for European *B. taurus* in a tropical environment. In a large Australian purebred-crossbreeding study from the Cooperative Research Centre for Cattle and Beef Quality, Newman et al. (2002) found that progeny from Belmont Red sires produced carcasses with the lowest sub-cutaneous fat and highest retail beef yield, desirable traits for human consumption. The above-mentioned research work with adapted genotypes has highlighted the importance of the synergy between natural and artificial selection for both adaptation and production traits.

The transition from unadapted to an adapted state for the N'Dama, Adaptaur, Senepol and Criollo could also involve elements of phenotypic plasticity, defined as the ability of a genotype to produce more than one phenotype in response to differing environments (Scheiner 1993; de Jong 2005; Fordyce 2006). Garland and Kelly (2006) point out that directional selection should support alleles that increase phenotypic plasticity in the direction of selection. When animal breeders are faced with multiple environments, models of phenotypic plasticity could contribute to the development of appropriate selection programmes for their production system (de Jong and Bijma 2002). It is conceivable that the Mexican Criollo from the Chihuahuan Desert³ possess alleles pertinent to plasticity for variations in water consumption, extreme fluctuations in ambient temperature, metabolism of a variety of herbaceous plants, and alternating between browsing and grazing. Existence of such alleles has implications for other semi-arid regions such as the livestock component in the management of dryland salinity of southern Australia as described by Masters et al. (2006). Given the extreme range of environments involved, plus the simultaneous natural and artificial selection pressure applied to achieve fitness, phenotypic plasticity could have contributed to the adaptation of the *B. taurus* to extreme and highly variable environmental parameters, and therefore future breeding programmes in variable challenging environments.

³A semi-arid region of the USA–Mexico border with an annual rainfall of 235 mL.

Extreme environmental conditions that result in high selection intensity on traits directly related to fitness have been shown to impact directly on the evolutionary process. Such high selection intensity tends to rapidly fix pleiotropic genes with predominantly positive effects (Lande 1982). Hoffmann and Parsons (1991) also point out that short periods (years, decades) of high selection intensity, rather than long periods (century or more) of low selection intensity, favour genes of major effect in the evolutionary process – hence the emergence of a major gene for 'slick hair' that contributes to heat resistance in the Senepol and Carora breeds (Olson et al. 2003). The identification and evidence of a putative major gene for tick resistance in the Adaptaur (Frisch 1994; Kerr et al. 1994) was not confirmed by Henshall (2004) with additional data and inclusion of polygenic effects in the statistical model. However, using complex segregation analysis, Kadarmideen et al. (2009) have shown evidence of major gene effects in this breed. The first large-scale gene expression profiling study (skin cDNA microarrays) was undertaken using resistant/susceptible Adaptaur cattle and identified several candidate mechanisms (e.g. antibody immune response day 1 of the infestation) that were involved in Adaptaur tick resistance (Wang et al. 2007). Nevertheless, because complex response mechanisms to multiple and variable stressors are involved, the contribution of quantitative genetics and molecular biology for the improvement of *B. taurus* to a stressful tropical and/or semi-arid environment remains to be fully assessed.

The completion of the bovine Genome Assembly (The Bovine Genome Sequencing and Analysis Consortium 2009) provides an opportunity to understand how cattle evolved and adapted to different geographical regions and production systems. The biological systems most affected by changes in the number and organization of genes in the cattle lineage include reproduction, immunity, lactation and digestion, all of which are important to our discussion on tropical adaptation. They concluded that these changes in the cattle lineage probably reflect metabolic, physiologic and immune adaptations due to microbial fermentation in the rumen, the environment and its influence on disease transmission, and the reproductive strategy of cattle. Indeed, understanding the taurine evolutionary trajectories also provides an insight into the predictability of cattle performance in cattle industries of the 21st century.

Genotype by environment by management interaction in cattle

Awareness of the taurine evolutionary trajectories in favourable environments will provide a guide to future

breeding experiments. Breeding goals are enhanced by not only knowledge about the diseases associated with production and the stress they cause but also mechanisms of resistance to diseases. Global warming, with elevated ambient temperatures, altered rainfall patterns and changed distributions of parasites and pathogens (Sutherst 2001; Howden et al. 2008; Thornton et al. 2009), will also impact livestock evolutionary trajectories (Burdon and Thrall 2008) and provide new challenges for livestock producers.

In the previous sections, we reviewed and discussed the evolutionary history and genetics of *B. taurus* cattle and the selection pressures imposed by different environments and/or production systems using tick resistance as a case study. In a systems framework, it is the interactions between genotype, environment and management that contribute to evolution of different genotypes. Compared to the tropically adapted *B. taurus*, the evolutionary history of temperate (productivism) *B. taurus* possess inherently higher levels of production potential, the production achieved in the absence of all environmental stress, and attributed to traits such as higher metabolic rates and appetites of the temperate taurine breeds. Conversely, the evolution of *B. taurus* in environmentally stressful regions has ensured that those genotypes possess mechanisms of adaptation (e.g. resistance to cattle tick) unlike their temperate counterpart (see Hoffmann and Parsons 1991). Hence, the metabolic rates of breeds such as Charolais and Angus would be higher than the tropically adapted breeds N'Dama and Criollo. However, in terms of adaptation to environmental stress the reverse is true and the N'Dama and Criollo possess relatively higher levels of environmental adaptation than breeds synonymous with productivism. Historically in commercial livestock production systems environmental stress is alleviated with strategies such as parasite control and supplementary feeding. Figure 2 shows the $G \times E \times M$ interactions in terms of relative production potential of temperate and tropical *B. taurus* (G) in the presence and absence of management (M) to negate the effect of increasing levels of environmental stress (E). The relative levels of production potential are shown on the vertical axis whilst the increasing levels of environmental stress are shown on the horizontal axis. Thus, as the level of environmental stress increases, the decline in production of the tropically adapted *B. taurus* is substantially less than the decline of the temperate *B. taurus* but if there is intervention to remove environmental stress then the response on production by the temperate taurine breeds would be greater than the response by the tropically adapted taurine breeds (Fig. 2). This implies that the costs associated with maintaining high productivity in temperate *B. taurus* might negate the profit obtained via

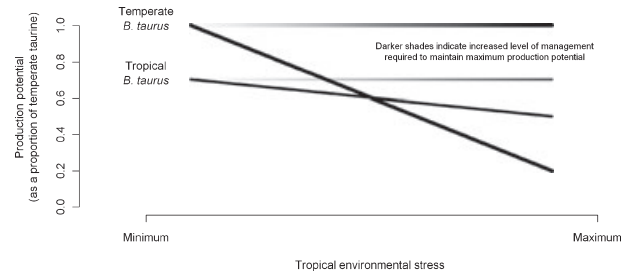


Figure 2 Diagrammatic representation of the $G \times E \times M$ for *Bos taurus* adapted to a temperate environment (e.g. Angus) and *B. taurus* adapted to a tropical environment (e.g. N'Dama) showing the proportional decline from optimal production potential for growth when there is no intervention by management to alleviate increasing levels of tropical environmental stress. The two shaded horizontal lines indicate the level of management required to maintain production potential.

high production. Hence, we emphasize that it is not high production, but rather 'production efficiency' that should be highest priority.

We have specifically avoided discussing $G \times E \times M$ interactions that exist within breed between animals at the level of genes which respond to different environments and/or different management interventions. These are extensively discussed in Kadarmideen et al. (2006a,b) and are outside the scope of this study. In practice, the major hurdle to achieving economic sustainability will be the acknowledgement that no single genotype will outperform all other genotypes regardless of environmental conditions. Moreover, interactions between genotype and management (e.g. use of acaricide to control cattle tick) occur when performances of different genotypes are not equally affected by different management inputs. Let us consider the following examples. If N'Dama and Angus cattle are given the same dosage of acaricide in a region of tick infestation, Angus cattle responds better to treatment than N'Dama cattle (response as in growth and fertility). If, however, N'Dama and Angus cattle are not given any treatment of acaricide in the same region, then N'Dama cattle are likely to achieve higher production performance than Angus cattle (Fig. 2). When different genotypes perform differently in different management strategies, then there is $G \times M$. Hence, a livestock system in essence is defined by the $G \times E \times M$ interactions and understanding $G \times E \times M$ and its impact on genetic, environmental and managerial strategies is crucial in future livestock systems.

Conclusion

Livestock production in the 21st century will be characterized by systems where both market (food and fibre

output) and nonmarket (social, environmental and climate change) issues are given consideration. Thus, live-stock producers will maintain their drive for maximization of output but with diminished reliance on industrialization and therapeutic agents to alleviate environmental stress and rely more on the genetic make-up of their animals to combat stress from heat, parasites, pathogens and poor nutrition. In other words, 'production efficiency' will become increasingly important. Various evolutionary trajectories of *B. taurus* since domestication suggest that the environmentally adapted breeds, along with *B. indicus* breeds, will play a pivotal role in the transition to sustainable production systems. The review of work on such breeds as the N'Dama, Senepol, Criollo and Adaptaur implies that both natural and artificial selection should be incorporated into selection decisions – assess potential breeding stock after a period of environmental stress. Once there is an understanding of the beef and dairy production diseases and the mechanisms of resistance to environmental stress then, as with the plant industries, molecular biology technology may be successfully applied to cattle. Corresponding breeding objectives for both production and adaptation traits could also be established via a combination of well-established quantitative genetic methodologies with emerging molecular biology technologies such as functional genomics.

We also conclude that the four adapted taurine breeds noted above, along with breeds that have undergone similar evolutionary trajectories, would possess candidate genes that could contribute to improving the productivity of cattle in challenging environments. However, the physiological antagonism between production potential and adaptation ensures no genotype achieves highest performance in all environments. The evolutionary history and knowledge of the genetic architecture will provide estimates of production potential (in a favourable environment) and level of resistance to environmental stress (in an unfavourable environment) and therefore estimates of how much production is realized when environmental stressors are controlled. Hence, the performance of a breed or combination of breeds in a given environment or degree of intervention by management to alleviate environmental stressors, are able to be predicted. Utilizing the full compliment of global cattle genetics and knowledge of $G \times E \times M$ interactions will help ensure sustainable levels of beef and milk production in the 21st century.

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