Relationships between adaptive and productive traits in cattle, goats and sheep in tropical environments

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ABSTRACT: This paper reviews the literature to determine the extent of genetic variation for resistance to stressors of tropical environments in beef and dairy cattle and goats and sheep. It also investigates the existence of genetic antagonisms that would preclude simultaneous improvement of productive and adaptive traits. Most adaptive traits are at least moderately heritable, meaning breeding to improve adaptation is feasible. It also appears that in cattle, goats and sheep which are well-adapted to the tropics, there are very few antagonistic correlations that would preclude simultaneous genetic improvement of both productive and adaptive traits to maximise herd profitability. The major constraint to genetic improvement of adaptation in tropical environments is the ability to accurately and cost-effectively record the fixed effects and phenotypes required for selection programs. Options to overcome this constraint are examined.

Keywords: stressors of tropical environments; genetic variation; cost-effective and accurate measurement

Background

Improving the productivity of livestock owned by large numbers of people living in tropical and subtropical regions (collectively referred to as tropical regions) throughout the world is a very high priority because those livestock comprise a major part of household income for some of the world's poorest people. FAO statistics show that in 2011, there were ~1.43 billion cattle, 0.9 billion goats and ~1.1 billion sheep with more than 65% of those animals grazed in the tropics (FAOSTAT, 2014; Table 1). These livestock make a major contribution to milk, meat and hide/fibre supply and additionally, in some regions, they are a major source of draught power and manure for use as fuel and maintaining soil fertility. Improving productivity and adaptation in tropical herds and flocks therefore must account for not only the use of existing and new genetic technologies but also their application to the specific socio-economic systems and the cultural values of the people who own them and who will benefit from the genetic improvement strategy (Payne and Hodges, 1997).

In this paper, tropical adaptation is defined simply as an animal's ability to survive, grow and reproduce in the presence of endemic stressors of tropical environments. This definition does not differentiate between resistance and tolerance to parasites as is suggested as necessary in several reports, though the authors acknowledge concerns that if animals are selected to improve tolerance rather than resistance, parasites will not be controlled and contamination of pastures may continue to be a concern. The economic implications for production systems due to lack of adaptation include production losses, mortalities, treatment costs where treatment is feasible and potential losses of markets (Burrow et al., 2001; Prayaga et al., 2006).

Table 1. Numbers of cattle, goats and sheep in different geographical regions of the world in 2011 and their percentage of the world total number (Source: FAOSTAT, 2013)

Continent	Number, million			Percentage of world total, %		
	Cattle	Goats	Sheep	Cattle	Goats	Sheep
Asia	4775.4	542.3	466.1	33.5	58.7	42.6
Africa	2763.6	321.5	304.7	19.4	34.8	27.9
Caribbean	92.2	3.7	2.7	0.6	0.4	0.2
Central America	469.4	9.2	8.9	3.3	1.0	0.8
North America	1048.4	3.0	6.4	7.4	0.3	0.6
South America	3509.6	22.2	73.1	24.6	2.4	6.7
Europe	1212.6	17.3	127.5	8.4	1.9	11.7
Oceania	392.6	4.9	104.2	2.8	0.5	9.5
World	14263.8	924.1	1093.6	100.0	100.0	100.0

This paper briefly reviews the role of resistance of cattle, goats and sheep to the stressors of tropical environments and highlights the genetic basis of those traits and their relationships with productive attributes. It also identifies current limitations to genetic improvement of adaptation of livestock grazed at pasture in the tropics and suggests alternative approaches that might enable some of the limitations to be overcome.

Environmental stressors. Livestock grazed at pasture in the tropics encounter numerous stressors including ecto-parasites (ticks; various fly species; other biting insects), endo-parasites (gastro-intestinal helminths or worms), seasonally poor nutrition, high heat and humidity and diseases that are often transmitted by parasites. Often the impact of each individual stressor on production and animal welfare is multiplicative rather than additive, particularly when animals are already undergoing physiological stress such as lactation. Under the extensive production systems common in the 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 (e.g. chemical treatments to control parasites generate concern about residues in meat products). As well, the parasites acquire resistance to the chemical treatments, creating additional parasite-control problems. The best method of reducing the impacts of these stressors to improve productivity and animal welfare is therefore to breed livestock that are well adapted to the stressors, overcoming the need for management interventions (Burrow, 2012). However breeding livestock for resistance to such stressors is at best very difficult and expensive in livestock populations in developed countries and is currently almost impossible in developing countries.

Measuring resistance of livestock to environmental stressors. Indigenous livestock which evolved in stressful tropical environments have a range of unique adaptive traits that enable them to survive and be productive in these environments (Devendra, 1987; Baker and Rege, 1994). In some cases the physiological basis of resistance or tolerance to environmental stressors has been well described, though more often, direct measurements of an animal's resistance to environmental stressor(s) are lacking. In those cases many studies simply infer 'adaptability' by measuring total herd/flock productivity, efficiency or net benefits of different breeds. This paper makes no attempt to interpret such 'adaptability' measures and examines only studies that have directly measured resistance to the various stressors.

For cattle, Burrow (2014) provides a detailed summary of a wide range of environmental stressors experienced by beef and dairy cattle grazed at pasture in tropical environments, the impacts of those stressors and the methods currently used to measure an animal's resistance to them (Table 23.1; Burrow, 2014). Current measurements include counts/scores of numbers of parasites based on either natural or artificial parasite infestations; lesion sizes due to biting or blood-sucking insects; rectal temperatures, coat colours and coat scores as measures of heat stress; differing measures of cattle temperament; and weight gain/loss. Of these measurements, only weights can be readily recorded during routine cattle husbandry procedures. The effects of various ecto- and endo-parasites include reduced feed intake and anaemia, but to date it has not been possible to effectively utilise haematological parameters as an alternative measurement of parasitism in cattle.

In goats and sheep, nearly all research on resistance of those animals to date has focused just on endoparasites, particularly the trichostrongyles. The most common trait to predict resistance to worms in goats and sheep has been faecal egg count (FEC) derived from either natural or artificial nematode infestations. Despite many documented reservations about the accuracy of FEC for this purpose, considerable experimental evidence shows that FEC is useful in differentiating the resistance/susceptibility status within and between breeds and strains of sheep (Eady, 1995). Packed red cell volume (PCV), a measure of anaemia, is another indicator of host resistance to endoparasites (Albers et al., 1987). Worm counts are the best measure of resistance to nematodes but involve slaughtering the animal. At least in young sheep less than one year of age, there is good evidence for a strong positive phenotypic correlation between FEC and worm burdens (Morris et al., 1995). The immunological mechanisms and parameters reflecting the underlying genetic resistance could potentially be used as phenotypic markers of resistance in sheep (Douch et al., 1996) but to date, no immunological parameters have been identified that are better predictors of resistance than FEC.

Breed types. In beef and dairy cattle, practical recommendations have been developed for cattle breeders, suggesting that for most purposes in the tropics, comparisons of animal performance should be made across general breed types or groupings (*Bos taurus* – British and European; *Bos indicus*; and tropically adapted taurine) rather than across specific breeds. This is because the substantial differences in growth, milking ability, reproduction and product quality evident between breeds in temperate environments are masked by the effects of environmental stressors in the tropics (Burrow et al., 2001; Burrow, 2006). The comparative performance of breed types for a range of productive and adaptive traits is summarised by Burrow et al. (2001). Use of tropically adapted breeds provides more cost-effective opportunities for beef and dairy cattle producers in tropical regions than British or European breeds, at least based on technologies that are currently available.

It is likely that similar recommendations could be developed for goats and sheep, but the evidence is less clear-cut than in cattle. Baker and Gray (2003) indicate that most breeds of goats and sheep identified as resistant or tolerant are tropical indigenous breeds, but many people perceive these relatively small breeds to be 'unimproved' with low genetic potential for increased production. Almost invariably, larger breeds with higher growth rates are assumed to be more productive and often the larger breeds are exotic breeds that are poorly adapted to the tropics. Baker (1998) reviewed the literature for between- and within-breed genetic variation for resistance of goats and sheep to gastrointestinal nematodes and concluded that much of the published research on breed characterisation for resistance suffered from poor experimental design. However based on a 6-year study in coastal Kenya, he concluded that Red Maasai sheep and Small East African goats were more resistant to worms (predominantly *Haemonchus contortus*) than Dorper sheep and Galla goats, with the resistant sheep and goats being 2-3 times more productive than susceptible breeds in a sub-humid Kenyan environment. In a more recent review, Bishop and Morris (2007) concluded that breed differences in resistance to nematode infections were well documented, particularly for tropical or sub-tropical sheep facing *H. contortus* challenge. Although many of the published breed comparison studies lacked power, they suggested there was good evidence in sheep for the Barbados Blackbelly, St Croix, Florida Native and Gulf Coast Native breeds (Caribbean and southern United States), Garole (India) and Red Maasai (Africa) breeds being relatively resistant cf. non-adapted breeds and this resistance translated into improved performance under many environmental conditions (Baker et al., 2004).

Similarly in goats, the West African Dwarf goat showed both trypanotolerance and resistance to nematode infections (Chiejina and Behnke, 2011). Kosgey et al. (2006) provide a good summary of known indigenous tropical sheep and goat breeds and their special attributes. Importantly, they indicated the dismal performance of breeding programs involving breed substitution of exotics for indigenous breeds and crossbreeding with temperate breeds had stimulated a recent re-orientation of breeding programmes in tropical countries to utilize indigenous breeds and crossbreeding to capitalise on heterosis where appropriate, along the lines of the recommendations developed for beef and dairy cattle (Burrow et al., 2001; Burrow, 2006).

Genetic variation for resistance to environmental stressors

To genetically improve traits through breeding, the traits being selected must be under direct or indirect genetic control. This section examines the heritabilities of various resistance traits (direct control), whilst the following section examines the direction and magnitude of genetic correlations between different traits (indirect control) to determine whether it is possible to improve resistance traits using easier-to-measure options and/or whether selection to improve resistance will result in unfavourable consequences in other traits due to genetic antagonisms between traits.

To date, there are relatively few reports of the heritability of the resistance of beef or dairy cattle to the stressors of tropical environments, probably due to the difficulties of measuring the very large numbers of animals required for such studies. Hence, most estimates currently available are derived from beef herds in tropical areas of northern Australia. Table 2 summarises the published ranges of heritabilities of resistance to ticks, worms, buffalo flies, heat stress, seasonally poor nutrition and temperament in beef and dairy cattle grazed at pasture in tropical environments.

As in cattle, there are relatively few published reports of the heritability of the resistance of goats or sheep to environmental stressors. Where such reports do exist, with few exceptions most are derived from studies of resistance to worms conducted in temperate environments in North America, Europe and Australasia (Baker and Gray, 2003). Bishop (2012) reviewed the literature for goats and sheep and reported that most heritabilities for FEC in sheep ranged from 0.2 to 0.4 with values in goats tending to be slightly lower, ranging from 0.1 to 0.35. Importantly though, resistance to the different strongyle parasites was strongly genetically correlated and close to unity. Even between strongyle and nematodirus FEC, genetic correlations were at least 0.5 (Bishop et al., 2004), indicating that FEC measures were useful indicators across different endoparasite species. Mandonnet et al. (2001) and Bishop and Morris (2007) reported that heritabilities for FEC differed in both sheep and goats, depending on the age of measurement, with FEC tending to be less heritable in kids and does. The Bishop (2012) review also indicated that PCV was heritable in sheep and goats and that Famacha© scores (an indicator of anaemia in the eyelid) were heritable in sheep. Additionally, the concentrations of various antibodies, eosinophils, pepsinogen and fructosamine were moderately to highly heritable and often strongly correlated with FEC.

Table 2. Range of heritabilities for different adaptive traits in tropically adapted beef and dairy cattle (Source: adapted from Prayaga et al., 2006 and Burrow, 2014)

Trait	Number of studies	Measure	h^2 range
Resistance to ticks	10	Tick count and tick score	0.05 to 0.44
Resistance to worms	6	Faecal egg count	0.07 to 0.57
Resistance to buffalo flies	3	Fly count and lesion score	0.04 to 0.36
Resistance to heat stress	6	Rectal temperature	0.12 to 0.33
Resistance to heat stress	6	Coat score	0.08 to 0.64
Resistance to seasonally poor nutrition	3	Dry season weight loss	0.14 to 0.34
Temperament	15	Haematological parameters	0.00 to 0.70

Due to the existence of at least moderate levels of genetic variation, both within and across breeds, for resistance to a wide range of environmental stressors in beef and dairy cattle and for resistance to gastrointestinal nematodes in goats and sheep, it is concluded that breeding to improve adaptive traits in these livestock species is possible. Initially breeding schemes to improve adaptation should be based on selection of appropriate breeds or breed types that are adapted to the local environmental conditions, before undertaking within-breed selection programs to improve resistance (Burrow et al., 2001; Burrow, 2006; Bishop, 2012). Based on recent reviews of the literature, genetic resistance to environmental stressors usually follows polygenic patterns of inheritance, as do the production traits (Bishop, 2012; Burrow, 2014), meaning that even if genomic testing options become cost-effective in future, it is likely that such tests will need to be fully integrated into quantitative genetic evaluation programs.

Genetic relationships between adaptive and productive traits

Not unexpectedly, there are even fewer estimates in the scientific literature of genetic correlations amongst various adaptive traits and amongst adaptive and productive traits than there are estimates of heritabilities for the adaptive traits. Knowledge of these genetic correlations is though essential for the effective design of breeding programs for livestock in the tropics.

Based on several different studies from northern Australia, Burrow (2014) concluded that selection of beef cattle to improve resistance to any one stressor of tropical environments would improve resistance to other stressors. This was particularly true for resistance to ticks, worms and heat stress, where genetic correlations amongst the traits were consistently moderately positive, suggesting the same or closely-linked genes affected all three traits. The same was 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 was largely independent of productive traits such as growth, reproduction and product quality, albeit the conclusions were drawn from a small number of Australian studies. Genetic correlations between resistance to heat stress and growth and reproduction traits from a number of different studies were generally significantly negative (favourable), reinforcing the fact of many genes in common between genes controlling growth and reproduction in the tropics and rectal temperatures when ambient temperatures are high. From these studies, Burrow (2014) concluded there were no major strongly antagonistic correlations between adaptive and productive traits that would preclude simultaneous genetic improvement of all the traits in tropical beef breeding objectives, providing the breeding program was based on tropically adapted breed types. The existence of significant genotype x environment interactions evident in non-adapted breed types reared in either tropical or temperate environments means this conclusion is not applicable in temperate breeds of cattle reared in the tropics (Burrow, 2012). Although there are no known data on the correlations between productive and adaptive traits in dairy cattle grazed in tropical environments, there is no reason to suspect this conclusion would not also apply to tropically adapted breeds of dairy cattle (Burrow, 2014).

There are no major studies known to have examined the genetic relationships between resistance to stressors of tropical environments and productive traits other than growth in either sheep or goats. In a review of small ruminant breeding programs, Bishop (2012) indicated the genetic relationship between productive traits and resistance to nematodes was often misunderstood, with incorrect inferences being drawn from observations that indigenous adapted breeds tend to be small with poor production characteristics, whereas high-performing exotic breeds often have poor disease-resistance characteristics. He concluded these breed differences were likely to simply reflect their selection history rather than reflecting genetic antagonisms between adaptive and resistance traits. Mandonnet et al. (2001) reported that genetic relationships between FEC and live weights in infected pastures were never significant, whilst genetic correlations between PCV and live weight decreased from 0.47 to 0.10 from weaning to 10 months of age, demonstrating the feasibility of breeding for improved resistance to nematodes without reducing growth rates in Creole goats. Bishop (2012) also reported that anaemia scores were consistently negatively genetically correlated with FEC and positively correlated with live weight in sheep (i.e. decreased FEC resulted in increased PCV and live weight gain), strengthening the evidence for a lack of serious genetic antagonisms between productive and adaptive traits in tropical ruminant breeding programs.

Opportunities to overcome constraints to genetic improvement of adaptive traits in the tropics

Options to genetically improve economically important traits in beef and dairy cattle and goats and sheep include within-breed selection, systematic crossbreeding and/or the use of composite populations. Where it is available, genomic information can also be used to improve the accuracy of selection within those options, rather than being used as an alternative method of genetic improvement. Although there are relatively few studies on which to base firm recommendations across differing livestock species, breed types and tropical environments and production systems, it appears from reviews of the literature that in cattle, goat and sheep breeds which are well-adapted to their production environment, there are very few antagonistic correlations that would preclude simultaneous genetic improvement of both productive and adaptive traits through selection to maximise herd profitability. The major constraint to livestock genetic improvement under commercial production systems in tropical environments is the difficulty and expense of accurately identifying appropriate fixed effects (e.g. contemporary groups) and measuring the full range of economically important productive and adaptive traits required to achieve a balanced breeding objective. We therefore examine these constraints and opportunities to address them in more detail in the remainder of this paper.

Fixed effects. Technology may provide the means of measuring animals and of estimating relationships, but it cannot replace the statistical imperative that, for the measurements to be meaningful, contemporary groups of appropriate structure and sufficient size are required. If the design is not adequate in terms of contemporary group size and structure, then measurements will not provide useful predictions of genetic merit and cannot contribute to estimates of heritabilities and correlations. Hidden stratification within contemporary groups can also be a problem. Because of the effects of dam age and previous lactational status on traits in young animals, measurement of these effects for use as covariates when analysing many production traits is almost essential. For adaptation traits, covariates such as previous exposure to a stressor may be important, and may be impossible to measure at an individual animal level. Design of the phenotyping program around existing contemporary group constraints is a cost-effective solution but may limit the range of traits.

An alternative is to establish livestock populations that are specifically designed to accurately manage and record animals within contemporary groups and capture data for the traits of interest. Examples of such populations in beef cattle are described by Upton et al. (2001) for growth, feed efficiency and carcase and beef quality and Burrow et al. (2003) and Johnston et al. (2012) for the full range of productive and adaptive traits in the breeding objective. Van der Werf et al. (2010) and Swan et al. (2012) describe similar populations designed to capture data for a range of productive attributes in meat and wool sheep. A large study in the USA has also developed specific populations to record resistance or susceptibility to Bovine Respiratory Disease in beef and dairy cattle (BRD CAP, 2014).

Phenotypes. If animals have individual electronic identification tags, technology offers potential to reduce the cost and increase the frequency of recording some production phenotypes. For example, walk-over-weighing (Richards et al., 2006) allows repeated measurements of weight, although Brown et al. (2013) concluded that, when used for nutritional management of sheep, current walk-over-weighing systems did not justify the investment in electronic identification. Technology-based systems to record adaptation traits have been proposed e.g. use of electronic nose technology to detect disease (Fend et al., 2005; Cramp et al., 2009). Given current costs in infrastructure, animal training and ongoing animal management, it may be some time before these systems will be cost-effective for recording adaptation traits on the large numbers of animals required for genetic evaluations.

Consequently, in the immediate future, phenotyping designs are likely to follow the approaches that have proved suitable for production traits: i.e. breeder-recorded phenotypes where available, augmented with central recording through progeny-testing facilities where required. Use of specifically designed industry-based livestock populations similar to those outlined in the previous section would also facilitate collection of phenotypes required for genetic improvement programs.

To date, only FEC has been considered as a commercially-relevant indicator of relative resistance to nematodes (Bishop, 2012) with actual counts or scores being used to genetically improve resistance to ecto-parasites. However, there are several indicator traits that could also be considered, for example:

- Measures of resistance: FEC, tick and fly count or scores, fly lesion size etc.
- Immune response: eosinophilia, antibodies such as IgA, IgG and IgM.
- Measures of impact of infection: anaemia, pepsinogen or fructosamine concentrations.
- Resilience: growth rate and required treatment frequency.

In future, collection of alternative phenotypes could become feasible with the development or adaptation of new technologies. Such options will be considered during the presentation of this paper.

Pedigrees and relationships. The need to record relationships amongst animals for genetic evaluation is the same for adaptation traits as it is for production traits. If production traits are already recorded on the same animals as adaptation traits, then no additional pedigree recording may be necessary. However it is the difficulty of the production systems in tropical environments that can make such recording an issue, not the issue of dealing with adaptation traits.

The benefits from knowledge of pedigree are well understood, allowing progeny test or BLUP-based selection in preference to selection on phenotype. In other than an intensive management system though, the costs are significant. Genomics offers a genuine alternative to the labour-intensive practices of single-sire mating and mothering-up. DNA-based parentage testing is effective in livestock through use of validated panels of markers for cattle, goats and sheep. The cost of the cheapest DNA assays on the market are now of the same magnitude as the cost of obtaining a tissue sample and of data management, and the cost of moderate-density SNP assays is not much more. With a thousand-SNP panel, parentage assignment is trivial. With a slightly larger (tens of thousands) SNP panel, it is not necessary to estimate discrete pedigrees at all (Meuwissen et al., 2001). In some circumstances, instead of using genomics to estimate the average phenotype for individuals in a family, it may be more cost-effective to estimate family contributions to groups of animals with the same phenotype using pooled DNA. A single assay on DNA assembled from the group of animals is sufficient to allow accurate estimates of family contributions, with the proviso the genotype of the families (or sire in half-sib sire families) is known (Kinghorn et al., 2010). Effectively this is equivalent to DNA parentage in parallel, estimating relationships for dozens of individuals from each DNA assay.

It is important to note that the technology required for estimating genomic relationships need not involve the latest high-density SNP platforms. For example, pedigree assignment has until very recently been exclusively conducted using microsatellite markers. A recently launched marker test for polled in beef cattle (Piper et al., 2014; Henshall et al., 2014) uses microsatellites to track haplotypes within and across breeds, effectively estimating relationships at a region of the genome. With appropriate statistical methods, microsatellites are completely adequate for many analyses and may be more cost-effective in many situations such as in developing countries.

Opportunistic genotyping and phenotyping. Often, a limitation with conventional selective breeding for adaptation traits in tropical environments is high year-to-year variability in the impact of stressors in commercial environments and low incidence of stressors in stud environments (e.g. due to parasite control or the stud may be located outside the tropics). Traditionally this problem has been addressed by running progeny test or experimental populations in an environment likely to produce variation in the trait of interest. In an example from a temperate environment, Greeff et al. (2014) observed variability in breech strike by managing sheep without preventative treatments for flies. An alternative approach is to opportunistically harvest phenotypes when and where natural variability exists. Bell et al. (2014) reported the collection of dag (faecal soiling) scores on close to 800 hogget sheep from a commercial property at a time when the full range of dag scores was expressed. Sheep in the commercial environment did not have pedigree records, so during phenotype collection, a blood sample was also collected and subsequently used to link the hoggets to sires used on the property, pooling blood samples within phenotype classes for the hoggets to reduce costs. Sires can then be linked to animals in the stud of origin and from there, to national genetic evaluation systems. This approach also offers great potential for sourcing records on easy-to-measure tropical adaptation traits that are not expressed in the stud environment, providing the contemporary group structure in the commercial herd or flock is suitable. In the commercial environment, where frequently large numbers of animals of common background are managed together, this may not be a problem, at least for traits that are minimally affected by non-recorded covariates having a genetic component.

Implications for livestock breeding programs in the tropics

Although there is a paucity of studies on which to base firm recommendations across differing livestock species, breed types and tropical environments and production systems, it appears that in cattle, goat and sheep breeds which are well-adapted to their production environment, it is feasible to simultaneously genetically improve productive and adaptive traits through crossbreeding and selection to maximise herd profitability. The greatest limitation to genetic improvement of these traits for the foreseeable future is likely to be the lack of accurate phenotypes on which selection can be based. Development of new technologies is now offering some potential for new approaches to overcome this limitation.

Literature cited

Albers, G. A. A., Gray, G. D., Piper, L. R. et al. (1987) Int. J. Parasit. 17: 1355-1363.

Baker, R. L. (1998) Anim. Genet. Res. Inform. 24: 13-30.

Baker, R. L. and Rege, J. E. O. (1994) Proc. 5th World Cong. Genet. App. Livest. Prod. 20: 405-412.

Baker, R. L. and Gray, G. D. (2003) In Sani, R. A., Gray, G. D. and Baker, R. L. (Eds) ACIAR Monograph 113 pp. 63-95.

Baker, R. L., Mugambi, J. M., Audho, J. O. et al. (2004) Anim. Sci. 79: 343-353.

Bell, A., Henshall, J. M., McCulloch, R. et al. (2014) These proceedings.

Bishop, S. C. (2012) Animal 6: 741-747.

Bishop, S. C., Jackson, F., Coop, R. L. et al. (2004) Anim. Sci. 78: 185-194.

Bishop, S. C. and Morris, C. A. (2007) Small Ruminant Res. 70: 48-59.

BRD CAP (2014) http://www.brdcomplex.org/ Accessed Feb 2014

Brown, D.J., Savage, D. B. and Hinch, G. N. (2013) Anim. Prod. Sci. 54: 207-213.

Burrow, H. M. (2006) Proc. 8th World Cong. Genet. App. Livest. Prod. CD Rom No. 32-01.

Burrow, H. M. (2012) Animal 6: 729-740.

Burrow, H. M. (2014) In 'The Genetics of Cattle' 2nd Ed. (Eds. D. J. Garrick and A. Ruvinsky), CABI, Ch. 23 (in press).

Burrow, H. M., Moore, S. S., Johnston, D. J. et al. (2001) Aust. J. Exp. Agric. 41: 893-919.

Burrow, H. M., Johnston, D. J., Barwick, S. A., et al. (2003) Proc. Ass. Advanc. Anim. Breed. Genet. 15: 359-362.

Chiejina, S. N. and Behnke, J. M. (2011) Parasites and Vectors 4: 12 (10 pp).

Cramp, A. P., Sohn, J. H. and James, P. J. (2009) Vet. Parasit. 166: 293-298.

Devendra, C. (1987) In Johnson, H. D. (Ed). World Animal Science B5. Elsevier pp. 157-168.

Douch, P. G. C., Green, R. S., Morris, C. A. et al. (1996) Int. J. Parasit. 26: 899-911.

Eady, S.J. (1995) In Gray, G. D., Woolaston, R. R. and Eaton, B. T. (Eds) ACIAR Monograph No. 34 pp 219-236.

FAOSTAT (2014) FAO Statistical Yearbook. http://faostat.fao.org/default.aspx Accessed Feb 2014

Fend, R., Geddes, R., Lesellier, S. et al. (2005) J. Clin. Microbiol. 43: 1745-1751.

Greeff, J. C., Karlsson, L. J. E. and Schlink, A. C. (2014) Anim. Prod. Sci. 54: 125-140.

Henshall, J. M., Piper, E. K. and Tier, B. (2014) These proceedings.

Johnston, D. J., Tier, B. and Graser, H-U. (2012) Anim. Prod. Sci. 52: 100-106.

Kinghorn, B. P., Bastiaansen, J. W. M., Ciobanu, D. C. et al. (2010) Acta Agric. Scand. Anim. Sci. 60: 3-12.

Kosgey, I. S., Baker, R. L., Udo, H. M. J. et al. (2006) Small Rum. Res. 61: 13-28.

Mandonnet, N., Aumont, G., Fleury, J. et al. (2001) J. Anim. Sci. 79: 1706-1712.

Meuwissen, T. H. E., Hayes, B. J. and Goddard, M. E. (2001) Genetics 157: 1819-1829.

Morris, C. A., Watson, T. G., Bisset, S. A. et al. (1995) In Gray, G. D., Woolaston, R. R. and Eaton, B. T. (Eds) ACIAR Monograph No. 34 pp 77-98.

Payne, W. J. A. and Hodges, J. (1997) In 'Tropical Cattle.' Blackwell Science, Oxford UK.

Piper, E. K., Tier, B. and Henshall, J. M. (2014) These proceedings.

Prayaga, K. C., Barendse, W. and Burrow, H. M. (2006) Proc. 8th World Cong. Genet. App. Livest. Prod. CD Rom No. 16-01.

Richards, J. S., Atkins, K. D., Thompson, T. et al. (2006) Proc. 26th Australian Soc. Anim. Prod. Short Comm. 32.

Swan, A. A., Johnston, D. J., Brown, D. J. et al. (2012) Anim. Prod. Sci. 52: 126-132.

Upton, W., Burrow, H. M., Dundon, A. et al. (2001) Aust. J. Exp. Agric. 41: 943-952.

Van der Werf, J. H. J., Kinghorn, B. P. and Banks, R. G. (2010) Anim. Prod. Sci. 50: 998-1003.