Breeding Objectives and Selection Traits for Extensive Beef Cattle Production in the Tropics

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SUMMARY

Breeding objectives are largely determined by market requirements. In the tropics, the overall breeding objective can be considered in terms of growth, reproductive rate, carcass quality, adaptation and temperament. Growth rate is a simple efficient selection trait. Reasons why potential increases in mature size are not as disadvantageous as in temperate areas are discussed. Reproductive performance has been less important in harsh than benign environments because of the later age of turnoff and higher drought risk of fertile cows. Current market trends towards younger slaughter stock highlight the need to identify marker traits in bulls for cow fertility. Adaptive traits have been defined for heat tolerance, parasite and disease resistance. It is not yet clear under what conditions direct selection for adaptation is likely to be advantageous. It may be appropriate where genotype - environment interactions need to be considered.

INTRODUCTION

In practical breeding programs, the realized rates of genetic improvement fall considerably below theoretical rates. The reasons for this are many and varied but one of the major factors stems from a lack of agreement by scientists and breeders on the relative importance of breeding objectives. A second factor is related to the problems associated with the translation of these objectives into practical breeding programs. Relatively few selection traits that are highly correlated to the objective and suitable for practical breeding programs have been defined, and objective measurement has been poorly accepted by the beef cattle industry, especially in the tropics.

It is not possible to precisely define breeding objectives for the tropics as a whole since they will vary with the different physical environments for each production and marketing system. Further, the marketing system is most industries is a dynamic one in which prices and costs are regularly changing. As a result, the relative importance of components of the breeding objective and therefore of selection traits will vary, often in an unpredictable way. Consequently, in this paper breeding objectives will only be discussed in general terms. Differences between objectives in tropical and temperate areas will be highlighted.

PRODUCTION SYSTEMS

There is a wide variety of production systems in the tropics. Throughout the tropics, production systems vary from fully intensive systems where land size is very small and animals are handled daily, to those based on extensive rangelands in which cattle are run at extremely low stocking rates and harvested on an annual or even less regular basis. Some of these systems
utilize the dual or multi-purpose nature of cattle, particularly those that predominates in lesser developed countries in the tropics. In these situations, cattle are not only kept for their meat, hides, horns and bones, but are often a vital source of draught power, milk, fuel, fertilizer and are even utilized for sport and recreation. Breeding objectives in such multi-product situations are extremely difficult to define since often little is known of the relative magnitude of inputs and outputs, including socio-economic factors which are often of overriding significance. Although feed-lot fattening operations are found in the tropics, they will remain a minor component because the grain required is also used by humans, a factor which will always keep prices high. In this paper discussion will be restricted to extensive or ranching beef production systems in the tropics using northern Australia as an example.

Environmental Factors

There are a number of factors, such as level of nutrition, heat and humidity, parasites and disease which account for the wide range of environments found in the tropics of Australia.

The restricted rainfall distribution combined with the high temperatures result in a short growing season. Rapid growth of pasture species in soils which are often low in fertility are responsible for low quality but usually ample quantity of forage. Because of the variation in feed supply from one season to the next, conservative stocking rates are employed. The use of improved pasture species, particularly legumes, has had mixed success. Tree legumes such as Leucaena and Glyricidia offer much promise for the future because of their deep root systems and general hardiness.

![Graph showing level of stress due to Heat (H), Nutrition (N) and Parasites (P) during different seasons in the humid and sub-humid tropics.](image-url)
Heat stress via the combined effects of temperature and humidity primarily affects appetite and activity of cattle. It is highest during lactation thereby leading to effects on reproductive rate (Turner, 1982).

Ectoparasites e.g. ticks, buffalo fly have a direct effect on animal production via blood loss, irritation and the immune response. Ticks are also carriers of diseases such as babesiosis and anaplasmosis while other vector born diseases include ephemeral fever and akabane. Endoparasites, principally gastrointestinal helminths are widespread in the tropics, as they are in temperate areas. However, the opportunity and economics of control are much reduced because of the relatively low value of each animal unit, large herd size and handling problems associated with extensive range conditions.

The physical environment in the tropics is highly conducive to the survival of pathogens and vectors of diseases. Accordingly, many diseases occur for which preventative or therapeutic measures do not exist. Treatment is often not feasible or economic for the reasons given above, especially where control of stock from neighbouring areas is poor.

The effects of the various stresses on the animal and production during the year are represented in Fig. 1. It can be seen that the environmental stresses are not constant but vary independently. During the dry season when temperature and parasitic stresses are lowest, nutritional stress is high. During the wet season when nutritional stress is low, animals unadapted to heat and/or parasites are unable to utilize the feed and suffer permanent losses in production. Prior to the wet season, growing animals often maintain or even lose weight due largely to the low quality feed. Adapted animals will recover much of this loss via compensatory gains in the following seasons. Adaptation to the environmental stresses is therefore an important requirement.

Marketing Systems

Market requirements have the major impact on breeding objectives. Breeders and producers must respond directly to both current and predicted market movements. In northern Australia, the grading system is based almost entirely on export market requirements. Components of a single carcass are sold to many different overseas destinations as well as on the domestic markets. The bulk of the export market is for U.S. manufactured beef. Because of the high slaughter cost per head, a premium is paid for large cattle. Large cull bulls and cows therefore achieve premium prices. A very small lucrative export market to Japan exists for carcasses weighing greater than 320 kg.

At present, no premium is paid for young females compared to older females. There is therefore no incentive to market heifers in preference to mature cows. Cull cows, being heavier, realize up to 30% higher values than heifers. Thus it is economical to breed a higher proportion of heifers and cull heavier cows for sale. It follows that longevity is a trait of little economic importance.

BREEDING OBJECTIVES AND THEIR IMPLEMENTATION

The common production goal for beef producers is to maximise the weight of beef of acceptable quality per unit of cost. Because markets are finite and prices fluctuate more than costs, Dickerson (1982a) argued that cost reduction may be more relevant than increases in productivity and associated profits.
Minimizing costs per kilogram of beef produced is usually compatible with optimizing productivity per hectare (Morris, 1979). A necessary qualification at the producer level for any objective is 'subject to an acceptable degree of risk'. The level of acceptable risk will depend on the financial structure of the enterprise, predictability of the seasons and attitude to uncertainty.

Most of the costs of production are associated directly or indirectly with the provision of feed. Activities include the clearing of land, sowing of improved pastures, application of fertilizer, fencing and capital costs of land. Because of the seasonal and annual fluctuations in feed supply and the impracticality of constantly varying stocking rates, the efficiency of utilization of feed in the tropics is low. Stocking rates are largely determined by the long term carrying capacity of the land with some minor adjustments in the short term. Therefore the system is less finely controlled than in temperate areas and the need for improved efficiency of feed utilization is reduced.

The major components of beef production are market liveweight, carcass yield and quality, reproductive rate and survival. In addition, the ease of handling cattle in extensive systems is important (Elder et al., 1980). Phenotypic and genetic variation in these components can be partitioned into two components (Frisch and Vercoe, 1984). Firstly, there is variation in the physiological and biochemical processes directly associated with the expression of the component trait. The second component relates to adaptation to the environmental stresses (nutritional level, heat, parasites and diseases). In simple terms, variation in adaptation largely affect the supply of nutrients to those processes directly involved in the expression of the components and therefore determines what proportion of potential or capacity is expressed. In stressful tropical environments, temperate breeds realize a smaller proportion of their potential production than Zebu breeds because they are less well adapted. Although the concept of potential and adaptation is a useful background to a discussion of breeding objectives, it is not of use in practice since objectives must relate to measurable traits. Adaptation can be defined and measured, but it is impractical to measure potential. Nevertheless, there are long-term implications if potential and adaptation are genetically antagonistic within a genotype, as Frisch and Vercoe (1984) suggest may be the case. Such a situation is considered later in the context of genotype-environment interactions. In the present discussion of breeding objectives attention is focussed on performance per se as well as on adaptation and temperament. Survival is largely a function of adaptational factors and so will be considered under that heading.

Breeding objectives are implemented in a breeding program through the choice of appropriate selection traits. To be useful, selection traits must be correlated to the objective, heritable, cost efficient and ideally, favourably correlated genetically with other traits. Simplicity is extremely important in the tropics where herd size is usually large and decisions must often be made on the same day as measurement because of the high cost of mustering. Labour is the greatest cost in implementing breeding programs. Consequently it is highly desirable for measurements to fit into normal commercial management practices. This often means that genetic gains will be lower than theoretical expectations. However implementation over larger populations will offset the shortfall.
Growth

Objective. In recent years, the usefulness of growth rate to market weight as a breeding objective has been questioned (Barlow, 1978; Dickerson, 1982a). Barlow (1984) even suggested that there was no sound basis for advocating selection for growth rate in maternal breeds and that a moratorium be held until a case is established. Concern is based on the results of a number of studies in a range of species which indicate that whilst increased growth results in higher gross efficiency (gain/feed intake) in growing stock, the higher maintenance costs of heavier breeding females leads to no advantage or even lower efficiency at the herd level (Dickerson, 1982a; Barlow, 1984). Certainly growth rate has been advocated widely as a breeding objective because it is easy to measure, results are readily visible and most producers have subscribed to the adage that bigger is better. To date there is no information on correlated changes in weights at later ages to selection for early growth in the tropics. However, it is difficult to see how a genetic increase in mature size is avoidable. Nevertheless there are a number of reasons why increased growth rate is desirable in tropical environments, despite potential increases in mature size.

Firstly, as outlined earlier, the supply of feed in the tropics varies from super-abundance to a restriction in qualitative rather than quantitative terms. In most years, surplus feed is burnt and therefore feed has a lower relative cost than in temperate situations. Secondly, maintenance costs of breeding stock are reduced in tropical environments by the negative environmental effects on mature size (Seifert and Rudder, 1976). The phenotypic effects of genetic increases in mature size and correlated changes in traits such as reproduction and survival are however unknown and need to be elucidated. Thirdly, at least in northern Australia, there is a substantial premium for large carcasses because many of the processing and marketing costs are on a per head basis. This applies equally to fat bullocks and cull cows. Thus, increases in growth rate, even if accompanied by increases in mature size, will be advantageous.

Clearly, there is a need to model the types of extensive production systems found in the tropics to try and quantitate the arguments presented above. Herd models, such as those developed at Texas A & M University have been useful in matching genotypes to production systems and to examine the effects of management changes on herd productivity (ILCA, 1978). Dickerson (1982b) outlined a method to account for direct and correlated genetic changes in such models, but at present estimates of the required phenotypic and genetic parameters are generally not available. Nevertheless, it is concluded that for the foreseeable future, increased growth rate is a valid breeding objective for the tropics.

Selection. Measures of growth are simple to obtain up to breeding age. The heritabilities of both pre-weaning and post-weaning growth rate are moderate to high (Table 1). At 18-24 months of age, dam age corrections and thus mothering are not required (Seifert, 1975). Seifert et al. (unpublished) found the genetic correlation between pre- and post-weaning growth to be low (+0.19), indicating that selection for growth to weaning is only moderately effective at increasing post-weaning growth. Maternal performance to weaning is highly heritable which is in agreement with the high repeatability of weaning weight (Seifert et al., 1982). It has been suggested that high milk production is correlated with lower cow fertility (Barlow, 1978). On the other hand, dairy breeds exhibit high levels of each trait. Preliminary results of studies in temperate areas suggest that high growth (Baker, 1983), where yearling weight have been increased, high milk production and increased in temperate areas (Koch et al., 1982a, 1982b). In tropical environments, increased milk production in the tropics is unlikely and is not desired.

Reproduction

Objective. Breeds exhibiting high growth in the tropics were generally crossing to improve fertility and production. However, increased growth rate will be advantageous in tropical environments. The model used by England for assessing genetic trends in dairy cattle (1983) and the estimates of heritabilities for milk production and reproduction in tropical environments (Seifert, 1983) are currently being used to develop an improved model for assessing genetic trends in tropical environments. This model is being used to improve fertility and production in tropical environments, with a focus on increasing milk production and improving fertility.
temperate areas show little change in reproduction following selection for growth (Baker and Morris, 1984). However, under some management systems e.g. where yearling mating is used, delayed age of puberty may be significant.

Estimates of the genetic correlation between growth to 24 months and birth weight have ranged from 0.59 (Seifert, 1975) to 0.23 (Seifert et al., unpublished), which are similar to those reported from temperate environments (Koch et al., 1982). With the exception of one set of lines in the U.S.A., increases in birth weight accompanying effective selection for growth rate in temperate areas have not been associated with increased dystocia (Baker and Morris, 1984). Furthermore, natural selection against dystocia is high in extensive management systems.

In temperate climates, selection for growth decreases fat content at a given weight, i.e. at a lower proportion of mature weight (Koch et al., 1982). Tropical studies have not been carried out but adverse changes are unlikely and will be overridden by environmental factors.

Reproduction

Objective. Higher reproductive rate in males and/or females leads to higher turnoff. Alternatively the same turnoff can be maintained with fewer breeders. In addition, higher reproductive rate permits greater selection intensity because of the surplus of breeding stock. There is greater scope for improving female fertility than male reproductive performance since multiple sire mating as used in commercial herds reduces the impact of individual bull fertility.

In intensive production systems, reproductive rate is one of the key factors in profitability. However, the relative importance is presently low in extensive tropical systems in Australia for a number of reasons. Firstly the age of turnoff is high, commonly ranging from three to five years, depending on the environment. The later the age of turnoff, the less important reproduction is as an economic trait. Taylor et al. (1980) concluded that if reproductive rate of the herd exceeds the minimum level required to maintain the herd in equilibrium, fertility is of less economic importance than growth. Secondly, in extended dry periods, and especially in droughts, the probability of lactating cows dying is higher than for non-lactating cows. Cows which calve regularly remain in relatively poor condition, and rarely have the opportunity to gain weight. During the dry season, highly fertile cows are 'high-risk'. Non-lactating cows function as insurance for herd, and therefore economic survival. Thirdly, the non-pregnant heifer is a marketable commodity. There is only a small price differential for sex, and heifers finish at a younger age and weight.

Because the reproductive rate is usually low in the tropics (Entwistle, 1983), there is clearly scope for improvement. However, the harsher the environment, the more fertility needs to be regarded as having an optimum, less than the maximum value, under current market conditions. The future trend in markets will be towards younger, heavier animals. The importance of fertility as a breeding objective will correspondingly increase as will the need for environmental improvements such as nutritional supplements and improved tropical pastures. In addition, the exploitation of heterosis for fertility using systematic crossbreeding programs may become more feasible under extensive grazing conditions as stock control improves and more suitable breeds become available. Although such systems have produced substantial gains over
straight breeding in temperate areas (Gregory and Cundiff, 1980), the benefits and practicalities have yet to be demonstrated in extensive production systems in the tropics.

Selection. Calving rate in adapted cattle is moderately heritable (Table 1). The estimates are higher than those reported for Bos taurus genotypes in temperate areas (MacNeill et al., 1984). Culling of infertile and subfertile cows is effective in making substantial phenotypic gains in herd fertility (Seifert et al., 1980). To date, no reliable measure of fertility prior to mating exists for heifers. However, critical weights to achieve given pregnancy rates can be defined (Rudder et al., 1985). Selection of the heaviest heifers will phenotypically improve fertility. No estimates of the genetic correlation between cow fertility and growth are available.

The major cause of low reproductive rate is lactational anoestrus, being greatest in first calf cows (Entwistle, 1983). Although hormonal measurements for ovarian activity are available, from a practical point of view, it is best measured by conception rate during a restricted mating period. Culling cows on this basis will improve herd reproductive rate (Seifert et al., 1980).

In a recent review, Entwistle (1983) concluded that no accurate measure of male fertility currently exists. Semen evaluation can detect clinically abnormal bulls but will not always identify lowly fertile bulls. Further, serving capacity tests developed with temperate breeds have so far shown poor correlations with paddock fertility (Christensen et al., 1982). Scrotal measurements are correlated to sperm production in Bos indicus genotypes (Wildeus et al., 1985) and to female fertility in Bos taurus breeds (Toelle and Robison, 1985), but the genetic relationship with either male or female fertility in Bos indicus genotypes is unknown. Recently, Post and Reich (1982) reported that plasma testosterone or luteinizing hormone levels following an injection of gonadotrophin releasing hormone were highly correlated with bull fertility. Preliminary results from follow-up studies showed a phenotypic correlation of only 0.35 (Hetzel, et al., unpublished), although the small size of mating groups restricted the variation in fertility in this study. Further investigations to evaluate potentially useful fertility markers in bulls are needed since the scope for selection pressure is considerably greater in males than in females.

Carcass Quality

Objective. Genetic differences between tropical genotypes in carcass traits such as dressing percentage, fat distribution, fat/muscle ratio have been reported (see Seebeck, 1984) but tend to be small. Whilst within breed genetic variation in tropical breeds has not been investigated, studies in temperate breeds (Swiger et al., 1965) indicate that it may be considerable. However, efficient use of carcass traits as breeding objectives is restricted by the lack of simple accurate live animal measurement techniques. At present, it seems that environmental methods e.g. altering the age of turnoff, processing procedures and the improvement of quality by increasing growth rate (Seebeck, 1984) are the most effective means of altering carcass composition to meet specific markets. Alternatively, where terminal crossbreeding is feasible between breed variation in carcass characteristics can be utilised.
In evolutionary terms, adaptation can be defined as the fit of an animal to its environment. However, where domesticated animals are farmed for meat productivity as well as survival is important. An alternative definition for adaptation could be related to the level of expression of genetic potential for productive processes. Adaptation is clearly not an all or none trait. Although Frisch and Vercoe (1984) found the Brahman to be more resistant to all the major environmental stresses in northern Australia than an unadapted Bos taurus genotype, it is more likely that breeds will have adapted to the specific environments in which they have evolved e.g. the adaptation of West African breeds to trypanosomiasis. In general, tropical beef breeds have not been extensively characterized for their adaptation to different environmental components. This type of information will allow better utilization of specific characteristics.

Clearly a certain level of adaptation is required for survival and production in tropical environments. Rising labour and treatment costs make it important to have easy-care animals. In many tropical areas, this has been achieved by crossing adapted genotypes, e.g. Brahman, Africander with Bos taurus breeds. However the question arises as to how to fine tune the level of adaptation, or whether in fact this is necessary, i.e. whether selection for production traits such as growth, will bring adaptation to the required level.

Frisch (1981) reported that response to selection for growth in Hereford-Shorthorn cattle in a tropical environment had arisen largely due to increased adaptability in terms of resistance to heat stress and parasites. However the starting level of adaptation was low in this genotype. What will occur in moderate or well-adapted genotypes? Such a study is currently underway at Rockhampton. It may be that although selection for growth directs significant selection pressure on adaptive traits, further improvement in some components is desirable. For example, since improved growth is associated with increased feed intake, more efficient systems for the dissipation of digestive and metabolic heat loads will be required, i.e. further selection pressure on heat tolerance by direct selection may be desirable. If selection for growth increases metabolic rate, maintenance requirement will be higher. This will be a disadvantage during periods of poor nutrition. Therefore it may be advisable to select animals capable of lowering metabolic rate under these conditions (Frisch and Vercoe, 1984).

Selection for production will act on genes for adaptation as well as those directly involved in the productive processes. Frisch and Vercoe (1984) have postulated that these two processes may be negatively correlated since breeds of high potential and high adaptability have not been identified and selection in an unadapted genotype appeared to result in an increase in adaptation but a decrease in potential (Frisch, 1981). However there is no evidence that high adaptation and high potential are physiologically incompatible so that it only remains to define such a breeding program to achieve this objective. Additional selection pressure for certain components of adaptation may be required in some environments.

Selection. In general, the heritability and, where repeated measures are made, repeatability are moderate to high for adaptive traits (Table 2). Permanent environmental effects are therefore relatively unimportant. The estimates cited are from Bos indicus cross populations. Most of the traits investigated thus
far are not as simple or cheap to measure as growth rate. Other adaptive traits correlated to production have been proposed but due to practical difficulties in measurement most have not been evaluated. Immunological measures of parasite resistance have been investigated. Products of genes in the bovine histocompatability complex may be useful as markers for this resistance (Stear et al., 1984).

Where economically viable vaccines, chemical treatments or nutritional treatments exist, it will not be appropriate to select directly for adaptation. Heat is one environmental stress for which non-genetic control is unlikely. However, the genetic option is becoming more attractive for parasite control as the demand for easy-care cattle increases.

The few genetic correlations between adaptive traits and production which have been reported are favourable. The correlation between rectal temperature and cow fertility was found to be -0.76 (Turner, 1982). Correlations between rectal temperature and growth to 18 months of age were zero in one group of heifers and -0.86 in another (Turner, 1984). In these cases around half of the variation in the adaptive traits and growth or fertility is common. However the remaining half is independent and may account for important additional variation which could be utilized by direct selection. Better estimates of the genetic correlations are required before the relative benefits of different selection programs using combinations of traits in selection indices can be evaluated.

Temperament

Objective. Under extensive management where cattle are rarely handled, temperament is a major problem for producers (Elder et al., 1980). While Zebu cattle are extremely docile and tractable under intensive management, they are often difficult to manage under extensive conditions. Although direct associations between behaviour and production are likely to be small, intractable animals add to production costs. Therefore temperament under extensive management should be considered as a breeding objective. A potential problem in improvement by breeding arises where breeding herds are managed more intensively than commercial herds. Behaviour in the two systems may be under different genetic control or behaviours in one system may not be exhibited in the other. It is difficult to determine the relative importance of temperament as a breeding objective because of the lack of quantitative information on its effect on production costs, but it is one of the major disadvantages of Zebu breeds cited by producers.

Selection. Fordyce et al. (1982) have quantified some of the temperament traits both in crush and yard situations. Of those investigated 'flight distance' appears to be the most heritable (Table 1). Its relationship to range behaviour and production traits appears to be favourable (Fordyce, 1984). Estimates of repeatability of this trait are around 0.75 (Fordyce, 1984), indicating a large permanent environmental component and therefore potential benefits from management strategies early in life. Investigation into more efficient, precise and accurate measures of temperament is needed.

GENOTYPE - ENVIRONMENT INTERACTIONS

Where diverse genotypes such as tropical and temperate breeds have been evaluated under widely differing environments, genotype-environment interactions have been large (Seifert, 1971b; Frisch and Vercoe, 1984). However, reported studies genetic environ env. env. env.
However, whilst within breed genotype-environment interactions have been reported in temperate areas e.g. (Burns et al., 1979), there have been no studies in tropical environments with adapted genotypes. So the question "is genetic improvement or superiority in one environment transferred to other environments?" remains unanswered. Where the stud breeding sector, for which the environmental level (e.g. nutrition, parasite control) is generally high, sells bulls to commercial producers, the question relates to the significance of sire x environment interactions.

The origin of between breed interactions appears to be largely due to the ability of the genotype to cope with environmental stresses such as heat and parasites. Frisch (1981) reported that response to selection largely for growth in an unadapted genotype in a tropical environment was due to an increase in adaptation at the expense of growth potential, implying a negative genetic correlation between the two components. If such a situation applied in adapted genotypes, selection in a harsh environment would result in genotypes which performed relatively poorly in good environments where adaptation is relatively unimportant and where potential was the limiting factor. The converse would equally apply. Further information on this question is required, and studies are in progress at Rockhampton. There are no good reasons to expect that adaptive traits are negatively correlated genetically to productive traits. Even if the correlations were close to zero, selection in a poor environment would not depress performance in a good environment. It is most likely that selection for growth in stressful environments will be effective in more benign environments, but that selection in benign environments without attention to adaptive traits may not be suitable for more stressful tropical environments.

IMPACT OF NEW TECHNOLOGIES

The development of new technologies is occurring at an ever increasing rate. It is unlikely that these technologies will greatly change breeding objectives but they will alter breeding methods. For example, developments in meat processing may reduce the need to consider meat quality in breeding programs. New and improved pasture varieties will improve the nutritional level, obviating the need to consider adaptation to low nutrition in many situations. The benefits of cheaper vaccines through the use of recombinant DNA technology may lessen the need for host resistance to parasites and disease. One potential danger is that such vaccines are used only in the more intensive stud breeding operations, further widening the environmental difference with commercial producers.

In the medium term it is more likely that new technologies will improve the efficiency of breeding programs and the rate at which objectives are met. Techniques such as embryo and egg transfer and embryo splitting are now available and will have some application in the extensive livestock industry. Other developments such as computerized marketing and meat classification schemes, electronic identification of stock, together with automation of weighing and drafting will greatly facilitate genetic progress.

The greatest promise undoubtedly lies in recent developments in molecular biology. The ability to now characterize individual animals at the DNA level is a major advance. Genetic markers identified by gene probes or as restriction fragment length polymorphisms (Soller and Beckman, 1982) will soon be available for disease and parasite resistance as well as production traits. Further it is now possible to contemplate the genetic engineering of
livestock, although assessing the possible impact is limited by our ignorance of the genetics of most production traits. Even when transgenic livestock become a reality, the task of the animal breeder will remain to match genotype and environment to achieve maximum productivity. In this respect, it will be even more important to define precisely what the breeding objectives should be for specific production systems.

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</tr>
<tr>
<td>Gastro-intestinal helminth resistance</td>
<td>Faecal egg count</td>
<td>Medium</td>
<td>Medium</td>
<td>0.27 - 0.68</td>
<td>0.82</td>
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<td></td>
<td></td>
<td>0.12 - 0.24</td>
<td>0.16 - 0.23</td>
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<td></td>
<td>0.31</td>
<td>0.04</td>
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<tr>
<td></td>
<td>Species egg count - Haemonchus</td>
<td>Low</td>
<td>High</td>
<td>0.60</td>
<td>-</td>
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<td>0.22</td>
<td>0.33</td>
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<td>0.29</td>
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<tr>
<td>Resistance to buffalo fly</td>
<td>Visual fly counts (Haematobia irritans exigua)</td>
<td>Medium</td>
<td>Low</td>
<td>0.25 - 0.71</td>
<td>-</td>
</tr>
<tr>
<td>Resistance to cancer eye</td>
<td>Eyelid pigmentation</td>
<td>Medium</td>
<td>Low</td>
<td>0.64</td>
<td>0.66</td>
</tr>
</tbody>
</table>

* a Field tick counts only  
* b Counts from artificial tick infestations