GENOTYPE (BREED) AND ENVIRONMENT INTERACTION WITH PARTICULAR REFERENCE TO CATTLE IN THE TROPICS
— Review —

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Summary

Genotype × environment (G × E) interactions must be understood if they are to be exploited to improve animal production, particularly in production systems associated with large environmental variations. The measurement and evaluation of G × E are discussed. Examples are presented that demonstrate G × E in different breeds of beef cattle for high temperatures, internal and external parasites and changes in quantity and quality of nutrition. It is demonstrated that productivity differences between genotypes or breeds under grazing conditions arise because of differences between genotypes in the combination of production potential and resistance to environmental stresses in relation to the levels of the relevant environmental stresses that are operating at the time. The F_1 cross between genotypes with high production potential (e.g. European *Bos taurus* breeds) and those with high resistance to environmental stress (e.g. Asian and African *Bos indicus* and sanga breeds) is an exceptional genotype with a unique combination of these two sets of attributes. The principles for G × E developed for beef cattle are briefly discussed in relation to dairy cattle, pigs, poultry and buffalo.

(**Key Words**: Tropical Beef Cattle, Heat, Parasites, Nutrition, Heterosis, Environmental Stress)

Introduction

Genotype environment interaction (G × E) means simply that the effect of the environment on different breeds or genotypes is not the same; this implies that there is no universally "best" genotype; the "best" genotype will vary from one environment to another and will depend on the prevailing environmental conditions.

G × E has special significance to both farmers and scientists. To the farmer it means using the particular breed or strain of animal that is most productive in his environment. To the scientist it presents the challenge of understanding whether genetic or environmental changes are the most efficient avenues through which productivity can be improved.

The more variable the environments in which production is required the more important the understanding of G × E becomes. In most intensive systems, e.g. pig and poultry and to a lesser extent dairy production, G × E is not as important as it is in extensive systems because in intensive systems environmental variables such as nutrition and climatic conditions and parasites and other diseases are closely controlled. It is in pastoral production systems such as those for grassfed beef and wool that G × E is evident and can play an important role in determining both the level of production and the strategies used for improvement.

G × E presents particular problems to the animal breeder. Selection procedures aimed at improving production in one environment may be counter-productive if the animals are to be used for breeding in different environments. Similarly, a cross breeding program that increases productivity in one environment may be ineffective or may decrease productivity in other environments. The only way these situations can be avoided is to understand the biological reasons why G × E occur. Equipped with this understanding, rational decisions can be made as to which animals are likely to be most productive in particular environments and how further

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improvements in productivity can best be achieved. Empirical testing is long term, costly and inefficient and has to be ruled out as a way of studying and utilizing G × E.

Examples of G × E

To illustrate the principles of G × E and to understand the biology of how it arises, the beef cattle model developed by studies on different breeds at the Tropical Cattle Research Centre, Rockhampton, Australia, will be used. The principles developed by this unique research approach can be extrapolated to other species and other production systems.

Beef cattle productivity is a function of fertility, mortality, growth rate and carcass composition. Two components of productivity are used to demonstrate the size and importance of G × E: growth rate in table 1 and fertility in table 2. In both tables the performance of 3 genotypes in 2 or more environments is shown. The genotypes are Brahman (B), a composite of closely related *Bos indicus* breeds; Hereford × Shorthorn (HS), an interbred cross between two *Bos taurus* breeds; F_1BHS, the F_1 cross between B and HS; and the F_nBHS, an interbred line of B × HS crossbreds. The growth rate of 3 of these 4 genotypes when grown in three different environments is shown in table 1.

TABLE 1. GROWTH RATE (KG / DAY) IN THREE ENVIRONMENTS DIFFERING IN THE LEVEL OF STRESS*

Breed	Low	Medium	High
HS	1.07	0.66	0.38
F_nBHS	0.90	0.69	0.53
B	0.81	0.63	0.56

* Source: Frisch and Vercoe, 1984.
HS = Hereford × Shorthorn interbred.
F_nBHS = Brahman × HS interbred.
B = Brahman.

The three environments represent different levels of environmental stress, low, medium and high. The low level of stress was created by housing the genotypes in shaded pens, feeding them *ad libitum* on a high quality roughage diet and maintaining them free of disease and both internal and external parasites. The medium level of stress was created by grazing the genotypes together but keeping them free of ticks and worms by dipping and drenching them every three weeks. Animals in the high level of stress were grazed with their dipped and drenched cohorts but received no anti-parasite treatment. Thus, the only difference between the medium and high level of stress was the control of parasites. These data show the complete change in ranking between the B, F_nBHS and HS in the different environments.

A different type of G × E is shown in table 2. The data are the average calving percentages for both lactating and dry cows of 3 genotypes in years of high and low overall calving percentage. In this instance there is not a reversal of the ranking but rather a change in the relative ranking. In years of high fertility the HS is very high, whereas the relative change between the years of high and low overall fertility is least in the B and intermediate of the F_nBHS. Note that this change in relative ranking in only evident for lactating cows. The fertility of non-lactating cows is similar for all breeds regardless of whether it is measured in years of overall high or low fertility. The fertility of the F_1BHS, not shown in the table, is the most resilient genotype to changes in environmental conditions. The data

TABLE 2. CALVES BORN (%) TO COWS THAT WERE LACTATING OR NON-LACTATING WHEN MATED IN YEARS OF ABOVE OR BELOW AVERAGE CALF CROP*

Breed	Above		Below	
	Lactating	Non-lactating	Lactating	Non-lactating
HS	78	78	47	75
F_nBHS	55	76	45	71
B	40	77	34	76

* Source: Frisch et al., 1987.
HS, F_nBHS, B = See table 1.

presented in table 2 demonstrate the existence and magnitude of G × E and illustrate its importance in determining beef production in different environments.

Measurement of G × E

Before attempting to understand the underlying principles of G × E it is necessary to understand the variables that need to be measured and the methods used in their measurement.

Tropical and sub-tropical environments are characterized by high temperatures and often high humidities, the presence of a range of external (ticks, buffalo fly) and internal (gastrointestinal helminths) parasites, diseases such as bovine infectious kerato-conjunctivitis (BIK), and large fluctuations in the quantity and quality of feed. It is necessary to have a measure of each of these factors, either in terms of the magnitude of the challenge or preferably in terms of their effect on the animals. Thus the effect of high temperature and humidity on an animal is measured through a rise in rectal temperature; a measure of whether the ambient conditions are causing a stress on the animal. The effect of other stresses is measured indirectly from estimates of resistance to each stress. None is a perfect measure of the effect of any strees but can be considered as a comparative index of the relative susceptibility or resistance of each breed to these potential sources of stress. Resistance to ticks is measured by counting the number of ticks greater than 4.5 mm diameter on one side of the animal (Turner and Short, 1972), resistance to gastrointestinal helminths (worms) is measured as the number of worm eggs per gram of fresh faeces (Roberts and O'Sullivan, 1950), and resistance to BIK is measured as a score in each eye on a scale of 1-6 with increasing severity of infection (Frisch, 1975).

The effect of each stress on the growth of any of the genotypes is proportional to their magnitude (Frisch and Vercoe, 1984). The effect of each of these stresses is manifested as a depression in weight gain or other components of productivity operating via effects on feed intake and utilization (Vercoe and Frisch, 1980).

Once indices of environmental stresses are available they can be used to assess the relative effects of these stresses on production of different genotypes. It is then possible to begin to understand how G × E arise and to develop strategies to either utilize their benefits or minimize their occurrence.

Understanding G × E

Responses to Heat Stress

A rise in rectal temperature causes a depression in appetite and an increase in protein catabolism (Vercoe, 1969). The effect of a similar increase in rectal temperature is similar for different breeds but the ambient temperature at which rectal temperature increases differs markedly between breeds. At about 25℃ ambient both Brahmans and HS have rectal temperatures of about 38.5℃. However, at about 33℃ ambient the HS have rectal temperatures of about 40℃. An ambient temperature of 39-40℃ is required to produce a 40℃ rectal temperature in the Brahman line. There is thus G × E associated with changes in ambient temperature.

Responses to Ticks and Worms

Ticks depress appetite and reduce dietary nitrogen utilization in both HS and Brahman based breeds (Seebeck, Springell and O'Kelly, 1971; O'Kelly and Kennedy, 1981). When different breeds are exposed to the same larval tick challenge, either in the field or by artificial infestation, Brahman and Brahman based breeds mature fewer ticks than HS, with Brahmans being the most resistant (Utech, Wharton and Kerr, 1978). A similar phenomenon exists for the gastrointestinal helminth, *Oesophagostomum radiatum* (Bremner, 1961; Vercoe and Springell, 1969). Because at similar larval challenges of external or internal parasites different breeds carry different adult parasitic burdens, the productivity of the breeds differs in the presence of those challenges and they respond differently to antiparasite treatments. When the three genotypes were grazed together, dipping and drenching resulted in a 111 kg increase in growth for the HS, 66 kg for the F_nBHS and 31 kg for the Brahman (Frisch and Vercoe, 1984). There is thus G × E in growth associated with the same parasite challenge.

Responses to Nutrition

When completely comparable Brahman, F_nBHS

and HS cattle were offered *ad libitum* feed in the abscence of strees, HS ate more and grew faster than Brahmans. The F_nBHS were intermediate for both intake and growth. When the same breeds were offered *ad libitum* a low quality (*c.* 1.2% N) pasture hay that just maintained liveweight level, the Brahmans maintained a higher weight, i.e. they had a lower maintenance requirement than HS, and again the F_nBHS were intermediate (Frisch and Vercoe, 1977; 1984).

Furthermore, when these genotypes were offered *ad libitum* a very low quality (less than 0.7% N) pasture hay, the Brahmans had a higher intake than the HS. There is thus G × E associated with diet quality. G × E also occur when the same genotypes are offered different quantities of the same diet (Frisch and Vercoe, 1977).

Interestingly, supplementing a very low quality roughage with rumen soluble N and sulphur caused a larger increase in intake of Angus (*Bos taurus*) cattle than of Brahmans (Hunter and Siebert, 1986). This, together with observed responses to diet quality, appears to be a consequence of higher levels of recycling of urea to the rumen of B and F_nBHS than of HS cattle (Vercoe, 1969; Hunter and Siebert, 1985a, 1985 b). Differential responses in different breeds to supplementation with urea and molasses have been observed in grazing cattle (Winks, Laing and Stokoe, 1972). There is thus G × E associated with diet supplementation.

The Integrated Story

Under field conditions all the environmental factors are operating simultaneously and it is to explain the G × E shown in tables 1 and 2 that the indices of stress outlined in this section play the key role.

In table 1 the ranking of the breeds for growth in the low stress environment is a consequence of the HS eating more than the F_nBHS and Brahmans. Relative intakes were 34.7, 29.3 and 28.2 g/kg for the HS, F_nBHS and Brahmans respectively (Frisch and Vercoe, 1984). Because these growth rates were measured in the absence of stress (no parasites or diseases, no heat stress and a high quality diet), these values represent the relative growth potentials of the genotypes.

At the high level of environmental stress the relative values of the indices of each stress for each breed are shown in table 3. The Brahmans had the lowest rectal temperature, had no BIK and carried the lowest tick and worm burdens of all breeds. The HS breed had the highest values for each index and the F_nBHS were intermediate. As a consequence, despite having the lowest growth potential, the B had the highest realised growth and the HS, despite its high growth potential, had the lowest growth rate. Growth in this environment was therefore determined, not by inherent appetite and growth, but by the proportion of the inherent levels that could be expressed in the presence of these stresses.

At the medium level of stress, generated by dipping and drenching representatives of each breed, the F_nBHS grew fastest although it had neither the highest growth potential nor the greatest resistance to stress.

A similar explanation can be sought for the interaction in reproductive rate illustrated in table 2. The years of above and below average calving rate can be equated with the levels of the various

TABLE 3. RELATIVE GROWTH POTENTIAL AND RESISTANCE TO STRESS OF THE F_1BHS RELATIVE TO PARENTS AND F_nBHS*

Breed	Growth potential (kg/d)	Resistance			
		Tick (No/side)	Worm (epg)	Temp (℃)	BIK**
HS	1.26	8.4	1600	41.4	3.43
F_nBHS	1.20	3.7	870	40.4	2.22
B	1.04	1.7	444	40.0	2.00
F_1BHS	1.30	2.1	550	40.3	2.00

* Source: Frisch et al., 1987.
** Score: see Frisch, 1975 Score 2.00 = both eyes clear.
F_1BHS = F_1 cross between B and HS.
HS, F_nBHS, B = See table 1.

stresses that operated during those years. The HS has the highest reproductive potential but can only express this advantage in years of low stress. On the other hand, the Brahman has a relatively low reproductive potential, but since the Brahman is relatively resistant to environmental stresses its reproductive rate changes little with variations that occur from year to year in the level of stress.

The HS genotype has been selected for growth rate in the presence of stresses for 25 years and, as a consequence, its resistance to ticks, worms, heat and BIK has increased dramatically. Fertility of this genotype has increased, not because of an increase in the inherent level, but because a higher proportion of its inherent level is now expressed (Frisch, Munro and O'Neill, 1987; Frisch, unpublished). Although growth rate in the presence of environmental stresses has increased, growth potential relative to a random breeding control line of HS has decreased (Frisch, 1981).

To summarise, G × E arises as a consequence of the differences in production potentials and resistance to environmental stresses of the genotypes under study. The larger the differences in these two variables the greater the potential magnitude of any G × E. Thus, G × E of small magnitude only can occur when genotypes with similar configurations of production potential and resistance to stress are compared, no matter how different the environments may be. The realised production of any genotype will depend on the magnitude of both its production potential and its resistance to stress and on the level of stress operating in the environment in which production is measured.

The Special Case of the F_1 Cross

Table 3 shows the relative growth potential and resistance to environmental stress and table 4 the relative calving rate in different environments for the HS, FnBHS, F_1BHS and Brahman. The F_1 has a level of growth potential that is similar to that of the HS, the parent with the higher growth potential, and levels or resistance to environmental stresses that approach those of the B, the parent with the higher levels of resistance to environmental stress. The two sets of characters required to maximise realised production, production potential and resistance to stress are uniquely combined in the F_1. The advantage of this combination relative to the other genotypes is illustrated diagrammatically in figure 1. Relative levels of growth potential are shown on the vertical axis and relative resistance to a combination of environmental stresses is shown on the horizontal axis; 0 represents no environmental stress and 1.0 represents very stressful environments in terms of ticks, worms, BIK, heat and nutritional variations.

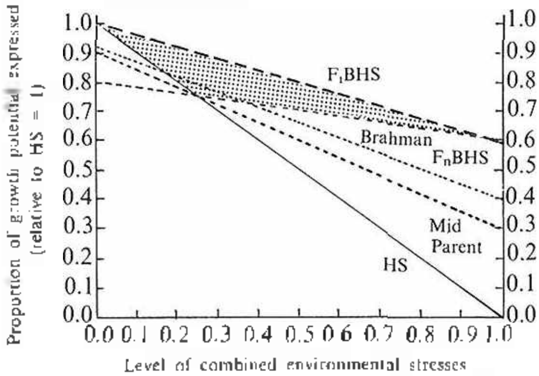

Figure 1. Diagrammatic representation of the G × E for *Bos taurus* (HS), *Bos indicus*, the interbred corss (F_nBHS) and the F_1 cross (F_1BHS) showing the decline in proportion of production potential expressed as the combined level of environmental stress increases. The shaded area denotes heterosis in the F_1 when heterosis is defined as the increase over the better parent.
Source: Frisch, 1987.

Different types of G × E are shown in the figure. The G × E between the Brahman and both the HS and F_nBHS is of the type where a complete reversals of rank occurs as the level of environmental stress changes. That between the Brahman and F_1BHS is of the type where the difference in realised growth between the genotypes declines as the level of environmental stress increases. That between the F_1BHS and HS is of the type where the difference in realised growth declines as the level of environmental stresses decreases. Note that although the interbred hybrid, the F_nBHS, has higher realised growth rates than both parents over only a small range of environmental stresses, the F_1BHS has the highest average growth rate over all environments and is superior to all other genotypes except in the most benign and most stressful environments. The characteristics of the different genotypes present a challenge to animal breeders; how can the desirable characteristics that underlie the superior performance of the F_1 be maintained in subsequent generations, i.e. how can the most appropriate combination of production potential and resistance to environmental stresses be maintained in subsequent generations?

Implications for Cattle Breeding

The major question raised by the negative relationships between traits associated with production potential and those with resistance to stress is whether there are underlying physiological reasons that prevent their combination in a way that will maximize realised productivity. Whilst arguments can be developed to suggest that the combination would be difficult, the high productivity and adaptive/productive configuration of the F_1 indicates that the physiological requirements for high production potential and high resistance to stress are not mutually exclusive. The question then becomes "How can high production potential and resistance to stress be combined through selection?"

It has been noted in the previous section that with selection for a character such as growth rate, which in a variable environment has antagonistic determinants, the best that can be achieved is some combination of production potential and resistance to stress that "on average" will be optimum. But the "average" environmental conditions possibly never occur in reality and in most years the combination is sub-optimal.

The only selection procedure that will eliminate or minimise fluctuations between years is to select independently for traits controlling production potential and those controlling resistance to stress. Other than on research stations, a selection program that identifies animals that not only have a high growth rate (feed intake) in the absence of environmental stresses (i.e. have a high growth potential) but also have a low maintenance requirement, high resistance to heat stress, internal and external parasites and diseases that cannot be readily controlled by vaccination would be impossible, and even on research stations such a program would require huge resources in terms of staff and facilities.

More practically, the growth of animals could be assessed in two contrasting environments, one of low stress and one of high stress. The growth in the low stress environment would be mainly a reflection of growth potential and in the high stress environment, a reflection of resistance to environmental stresses. Individuals that ranked highly in both environments would be those for use in subsequent breeding. One deficiency in such an approach is the unknown effect of compensatory gain and its possible bias towards different animals. If animals were ranked first in the stressful environment and subsequently in the low stress environment, some individuals would perform well in the latter merely because of compensatory gain. Given the complexity of any selection program aimed at maximising the two sets of determinants of realised productivity, crossbreeding is likely to be a more viable and achievable alternative for maximising realised productivity in stressful environments.

As noted earlier, the F_1BHS has the growth potential of the HS parent and is as resistant, or almost as resistant, as the B parent. This combination is responsible for the fact that the F_1 outperforms both parental types in all but very low stress and very high stress environments. This reduces the variation from year to year in realised productivity.

The problem is to maintain the characteristics of the F_1 in subsequent generations. Backcrossing to the parent with the high production potential will reduce realised productivity because of a reduction in resistance; backcrossing to the resistant parent will reduce realised productivity because production potential is reduced; interbreeding reduces realised productivity because the F_2 tends towards the mid-parent mean for both production potential and resistance to stress. A theoretical alternative is to cross the F_1 to a third, unrelated breed that has moderately high levels of both resistance and production potential. With this in mind, Australia has imported the Boran (African *Bos indicus*) from Zambia and the Tuli (a Sanga type) from Zimbabwe, breeds that are distantly related or unrelated to the Asian *Bos indicus* breeds from which the Brahman is derived and which have, because of their evolutionary history, high levels of resistance to stress coupled with relatively high levels of fertility.

Apart from the practical applications that these importations have in terms of direct benefit to beef producers in stressful tropical environments, they will also enable further testing of the hypothesis proposed by Frisch (1987), namely that the productivity of the F_1 can be predicted from the performance at breeds and the characteristics of the parent. If this hypothesis, based on the analysis of the B, HS and the F.BHS, is upheld by testing it in different crosses, then the development of crossbreeding strategies can proceed rationally and their outcome predicted with certainty. This in time will enable productivity to be improved and the problem of G × E considerably reduced.

Examples of G × E Interactions in Other Species

Most dairy cattle, pigs and poultry used for commercial production in temperate regions are reared under conditions that are designed to minimise the effects of the environment on production. Diseases and parasites are controlled, the animals are housed to reduce the effects of climatic stresses and well balanced, high quality diets are offered to the animals. Consequently, within a region, G × E interactions become evident when temperate strains or breeds of these species are transferred to stressful tropical regions.

Dairy Cattle

There is a marked decrease in milk yield, survival, growth and reproductive rates relative to those achieved either in temperate regions or by crossbreds based on temperate dairy and zebu breeds, when temperate dairy breeds are transferred to stressful tropical conditions. For example, Vaccaro, Cardozo and Vaccaro (1983) reported that for Holstein heifers introduced from the USA into the lowlands of Venezuela, 8% of the heifers and 81% of their calves had died within a year, the heifers had a high incidence of mastitis and foot and leg problems and they produced less milk than European × zebu crossbreds on the same farm. The high potential of the Holsteins for milk production could not be expressed because of their lack of resistance to the stresses of the production environment. On the other hand, because the crossbreds have lower milk yield potential than the Holsteins, they would produce less milk than the Holsteins if both were compared in temperate regions.

Pigs

Because of the method of rearing of commercial pigs, it would be expected that most investigations of G × E interactions would involve nutritional differences. An early study (Fowler and Ensminger, 1960) reported G × E interactions between pigs selected for high gains on either *ad libitum* or restricted feeding. The study showed that selection on the two planes of nutrition was for two distinct genotypes. Selection on restricted feeding increased the efficiency of feed conversion but selection on *ad lib.* feeding increased appetite. Thus, pigs selected on *ad lib.* feeding grew slower on restricted feeding than the pigs selected on restricted feeding. This and other studies (see review by Pani and Lasley, 1972) have produced strong evidence for the differential responsiveness of pig genotypes to high and low feeding levels.

Poultry

The same strains of egg or meat producing poultry are used commercially throughout the world. This could be taken to mean that G × E interactions are not important in either form of production. However, most commercial poultry flocks are housed and the environments in which they are reared are more closely controlled than for any other domestic animal. The economic importance of G × E interactions under these conditions is therefore likely to be correspondingly less. However, egg production by different breeds and strains has been reported (see review by Pani and Lasley, 1972) to respond differently to different systems of housing and to other environmental factors. Differences between strains in resistance to diseases and heat stress have also been reported (Loc. cit.). Comparisons of strains of different disease resistance under conditions where disease resistance is important (such as most tropical village situations) would therefore be expected to favour the disease resistant strains. However, strains that have high antibody responses are smaller and have lower efficiency of feed conversion than poultry that have lower antibody responses (Gross and Siegel, 1988) and comparisons in the absence of disease could be expected to favour less resistant strains.

Buffaloes

Published reports of G × E interactions for

TABLE 4. PROPORTION OF COWS OF DIFFERENT GENOTYPE PREGNANT IN DIFFERENT ENVIRONMENTS*

Level of environmental stress	HS	F_nBHS	B	F_1BHS
Low	0.94	0.77	0.62	0.89
Medium	0.67	0.61	0.51	0.81
High	0.32	0.45	0.34	N.A.

* Source: Frisch et al., 1987; Frisch unpublished.
HS, F_nBHS, B, F_1BHS = See table 3.

buffaloes are almost non-existent. This does not mean that G × E interactions are unimportant but rather that their occurrence has not been sought. More recently (see Frisch, 1989) comparisons of swamp and river types with their crosses reared in contrasting environments have been initiated. These studies will allow both the detection of any G × E interactions that affect productivity and the assessment of their importance in the improvement of productivity of the domestic buffalo. A preliminary report from the dry zone of Sri lanka (Mohamed, 1989) of calving to conception intervals of Lanka (swamp) and Murrah (river) cows illustrated that G × E interactions are likely to be an important consideration in buffalo improvement (table 5). While the *post-partum* interval of both breeds was markedly reduced by supplementary feeding with concentrates, not only was the interval achieved by the unsupplemented Lanka cows similar to that achieved by the supplemented Murrah cows, but the responsiveness of the Lanka cows to supplementary feeding was also greater (a reduction of 128 days) than that of the Murrah cows (99 days reduction).

Even within a country, the environments in which sheep are reared are far less controlled than those used for pig, poultry or dairy production. The importance of G × E interaction is therefore expected to be correspondingly greater. This is reflected in the use of different breeds in dry or wet areas-differences in susceptibility to fleece rot, foot rot or internal parasites can have a marked bearing on which breeds can be used successfully in any given area. In the extreme case all or most animals of one genotype may succumb to an environmental stress while other genotypes are relatively unaffected. Such an instance has been reported from Kenya where the indigenous Red Masai sheep were compared to six exotic breeds in areas where *Haemonchus contortus* was endemic (Preston and Allonby, 1979). No attempt was made to control intestinal parasites. Under these conditions, all exotic breeds, but none of the indigenous Red Masai, suffered mortalities. Within 26 weeks after their introduction to worm infested pasture, all Hampshires had died. The differences in mortalities were directly attributable to differences in resistance to *H. contortus*. The Red Masai was the most resistant breed as assessed either by faecal egg counts or adult worm recovery at necroscopy. In this case the G × E has arisen because of the differences between the lines in their capacity to cope with a major environmental stress viz. *H. contortus*. Superior production potentials of the exotic are then quite irrelevant in the production system used.

TABLE 5. G × E IN RECONCEPTION INTERVAL IN LANKA AND MURRAH BUFFALO COWS*

Environment	Calving to conception interval (d)	
	Lanka	Murrah
Grazing	214	313
Grazing + supplements	76	214

* Source: Mohamed, 1989.

Conclusions

The G × E that occur when different genotypes are transferred between different environments arise because those genotypes differ in genetic potential and resistance to the stresses operating in the different environments. Knowledge of why G × E occur not only allows a rational choice of genotypes best suited to a given environment or production systems but also leads to an improved understanding of how productivity can be most efficiently improved in any given environment. G × E can be be eliminated either by completely eliminating environmental stresses or by using animals that are completely resistant to environmental stresses. The intensive pig and poultry industries have adopted the former approach and have concentrated on improving genetic potential as the way towards improved productivity. The beef cattle industry in particular still relies on the latter approach and resistance to environmental stresses is, and is likely to remain, an important consideration in extensive pastoral systems.

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