Sire by finishing environment interactions for beef cattle carcass and meat quality traits

P.L. CHARTERIS, D.J. GARRICK AND S.T. MORRIS

Department of Animal Science, Massey University, Palmerston North, New Zealand.

ABSTRACT

Genotype by environment interactions can result in bulls having different genetic merits applicable to different environments. Beef cattle have traditionally been finished on pasture in New Zealand. The desire to meet perceived market requirements for meat quality has encouraged progeny testing and led to feedlotting. The objectives of this study were to evaluate sires on the basis of performance of their pasture-finished steer progeny, their feedlot-finished steer progeny and to compare the assessments of these sires from offspring in each environment. Fourteen Angus sires had progeny in both environments comprising 54 pasture-finished steers and 148 feedlot-finished steers. Estimated Breeding Values (EBVs) of each sire were obtained separately for eight traits that were measured for both pasture and feedlot progeny. Product-moment correlations between sire EBVs based on pasture-finished progeny and EBVs based on feedlot-finished progeny averaged 0.11 (range -0.16 meat colour to 0.50 subcutaneous fat depth).

The expected distributions of these correlations between EBVs were obtained by simulation for a range of null hypotheses determined by the true genetic correlation between performance in the two environments using Monte Carlo simulation. The expected distributions of correlations between environments were determined for differing numbers of progeny per sire and for the effect of preselecting prior to entering the progeny test. The distributions of correlations were used to determine whether the low observed correlations between EBVs estimated from each environment were likely to have arisen from chance sampling or were truly indicative of genotype by environment interaction. Based on actual progeny numbers per sire in each environment there were significant (P=0.05) sire by finishing environment interactions for most traits analysed. Increasing the number of progeny per sire would increase the chance of detecting such interactions, in that case separate progeny testing programmes for each environment may be necessary.

Keywords: Angus; progeny test; feedlot; pasture; genotype by environment interaction.

INTRODUCTION

A genotype by environment (GxE) interaction exists when phenotypic differences due to genotype differ from one environment to another. Such interactions are more commonly found when animals with large genetic differences are compared in very different environments (Hohenboken, 1986). Less evidence exists as to the importance of interaction between small genetic differences and large environmental differences. If small genetic differences, such as loci within an individual interact with large environmental differences in influencing the phenotype of animals evaluated, then the prediction of breeding values (BVs) of those animals will vary according to the environment in which they are evaluated. GxE interactions are important considerations for genetic selection since animals evaluated in one environment may rank differently or the magnitude of differences in genetic merit between them may change when evaluated in another environment (Dickerson, 1962; Bondoc and Smith, 1993). Failure to account for GxE effects may result in sub-optimal genetic gains or genetic change in an undesirable direction. This re-ranking will be of importance for sire selection across countries if a low correlation between sire EBVs between countries result from largely different environments or breeding objectives in these environments (Buchanan and Nielson, 1969; Hohenboken, 1986).

The aim of this study was to quantify the size of sire by environment interactions using data from a New Zealand Angus progeny test in which sires were evaluated for carcass and meat quality traits based on pasture-finished and feedlot-finished progeny records. Second, the likelihood that observed correlations between EBVs arising from progeny records in different environments resulted from a true GxE interaction was determined.

MATERIALS AND METHODS

Carcass data collection

Live weight and carcass records were obtained for 202 steers from the N.Z. Angus Carcass Evaluation and Progeny Test (ACEPT). All steers were identified by sire. There were four contemporary groups, defined by herd of origin and date of slaughter, two comprising feedlot-finished progeny and two of pasture-finished progeny. Hot carcass measures were made at the time of slaughter with meat quality traits assessed following a period of chilling of 24 hours. Meat quality traits including marbling (BMS), fat colour (BFS) and meat colour (BCS) were assessed by visual comparison to known standards whilst carcass weight, eye muscle area (EMA) and subcutaneous fat depth were measured objectively.

Estimation of genetic merit

Progeny records were analysed using mixed model procedures to obtain Best Linear Unbiased Predictions, BLUP (Henderson, 1972) of genetic merit of 23 sires for

growth, live weight, carcass and meat quality traits. Details of test design and progeny numbers across contemporary groups and sires are shown in Garrick *et al.*, (1994). Fourteen of these sires were represented by both pasture-finished and feedlot-finished progeny. Those sires having progeny in both environments had an average of 11.5 feedlot-finished and 4.6 pasture-finished progeny each. Sires estimated breeding values (EBVs) were reported separately based on progeny records in each environment. Accuracy of sire evaluation was expressed as the correlation between true and estimated genetic merit (r_{TI}), using Best Linear Prediction (BLP) methodology, (Van Vleck *et al.*, 1987). Standard error of prediction of EBVs was given as SEP $=\sigma_g \sqrt{1-r_{TI}^2}$ where σ_g is genetic standard deviation.

Correlation between EBVs for sires evaluated separately from both pasture or feedlot finished progeny records

Product-moment correlations between EBVs provides an estimate of the genetic correlation between the same trait in different environments (Falconer, 1952). Rank correlation was calculated as the correlation between sires ranking based on their EBVs evaluated from two environments. Observed correlations between EBVs in such situations are usually less than one, however, the expected value of the correlations is also less than one, even if the underlying genetic correlation is unity (Notter and Diaz, 1993). Thus, to reject the null hypothesis H_o: $r_G = 1.0$, that is, no GxE interaction exists, correlations between EBVs for the 14 sires should be compared with the expected distribution of sample estimates. The expected correlation between EBVs of 14 sires (for actual progeny numbers) was determined using Monte Carlo simulation. The distribution of expected correlations between EBVs of sires estimated in two environments were as follows:

1. A random sample (n=14) was taken from a normally distributed population ~N(0,1), to obtain a true breeding value (BV_i) for each of 14 sires (i = 1,...14)
2. EBVs for each of 14 sires based on pasture and feedlot finished progeny records (assuming an average of 4.6 pasture-finished progeny per sire n_P and 11.5 feedlot finished progeny per sire, n_F), EBV_P and EBV_F were estimated for $h^2 = 0.25$, as:

$$EBV_{Pi} = BV_i \left(\frac{n_p}{n_p + 15}\right) + \left(\frac{15n_p}{n_p + 15}\right) hZ_i \quad [1]$$

$$EBV_{Fi} = BV_i \left(\frac{n_F}{n_F + 15}\right) + \left(\frac{15n_F}{n_F + 15}\right) hZ_{i'} \quad [2]$$

   where: Z_i and $Z_{i'}$ are two independent random numbers drawn from a normal distribution ~N(0,1). Derivation of equations 1 and 2 are shown in Appendix One.
3. Product-moment correlation between EBV_{Pi} and EBV_{Fi} was calculated.
4. Steps 1-3 were repeated for 1000 iterations to obtain the mean (expected) correlation between EBVs based on given numbers of progeny records per sire under repeated random sampling.

Expected correlations between EBVs were derived in steps 1 to 5 to test the null hypothesis that $r_G = 1.0$. Further simulations assumed an r_G of 0.3, 0.5, 0.7 and 0.9. This involved replacing step 1 with a bivariate normal sampling strategy. Increasing numbers of progeny evaluated per sire increases the accuracy of sire breeding value estimation resulting in a higher expected correlation between EBVs than for lower progeny numbers. For each r_G (0.3-1.0) the correlation between sire EBVs was determined for different numbers of feedlot and pasture-finished progeny (n_F and n_P respectively). Simulations were for equal numbers of feedlot progeny per sire (n_F and n_P = 20 to 1000) and for unequal progeny numbers per sire across environments (n_F and n_P = 10:5 to 30:10).

An assumption in Step One is that a random sample is taken from a normal distribution to obtain a true BV of sires entering the progeny testing programme. In practice, due to costs and time delays associated with progeny testing, sires are usually selected prior to entering a progeny test. Further analysis was undertaken assuming bulls had been selected on their own estimated genetic merit prior to entering the progeny test. A random sample of bulls (n=14, 20, 50, 100, 1000, 2000, 5000) were drawn from a normal distribution ~$N(0,\sigma^2_g)$ to obtain true BVs for each of n bulls in the population. For each sample of bulls, the 14 highest genetic merit bulls (EBVs calculated from one record on each bull, $h^2 = 0.25$) were selected to enter the progeny test. The true BV for each of these 14 selected bulls was inserted into step 1 (above) using actual progeny numbers. Steps 1 to 5 were repeated for each proportion of bulls selected. The EBVs of candidate bulls to enter the progeny test were estimated as:

$EBV = 0.25\ BV_i + \frac{3}{8}\ Z_{i''}$ where: $Z_{i''}$ is a random number drawn from a normal distribution ~N (0,1).

RESULTS AND DISCUSSION

Liveweight, carcass and meat quality measures

Phenotypic means and variance for most traits were higher for feedlot-finished than pasture finished steers, however steers finished on pasture had both higher mean dressing percentage (+5.82%) and eye muscle area (+55.88 cm^2) than feedlot finished steers. There were differences between carcass measurements with carcasses from feedlot-finished cattle being cut between the 6th and 7th rib, (the site of preference for estimating yield of carcasses for the Japanese beef market) whereas measurements were made between the 12th and 13th rib for pasture-finished steers. Progeny in different environments were slaughtered at different carcass end-points (carcass weight and fat depth). A valid comparison of sires between environments may require adjustment to constant end-points (either carcass weight or fat depths).

Actual correlations between sire EBVs

Observed correlations between EBV_P and EBV_F ranged from -0.16 for BCS to 0.50 for subcutaneous fat

depth (Table One). Rank correlations for sire EBVs ranged from -0.13 (BFS) to 0.46 (subcutaneous fat depth). For five of the eight traits evaluated, rank correlations for sires were negative suggesting re-ranking of sires when progeny were evaluated based on records from feedlot or pasture-finished progeny.

TABLE 1: Correlation and rank correlation between EBVs for sires whose progeny were evaluated on both pasture and feedlot

Trait	EBV Correlation	Rank correlation
Carcass weight (kg)	-0.15	-0.02
Dressing percentage	0.34	0.40
Beef Fat Standard (BFS, 1-7)	0.03	-0.13
Meat pH	0.19	-0.10
Beef Marbling Std. (BMS, 1-12)	0.23	0.35
Eye muscle area (cm2)	-0.08	-0.09
Subcutaneous fat depth (mm)	0.50	0.49
Beef Colour Std. (BCS,1-7)	-0.16	0.0
Mean	0.11	0.11

Product-moment correlations between sire EBVs in the present study were lower than correlations between sire expected progeny differences (EPDs) for weaning weight in Hereford cattle evaluated in different regions of the United States, range 0.30-1.0 (Bertrand *et al.*, 1985) and for correlations of sire EBVs between regions within the United States, for birth and weaning weight in Simmentals (Buchanan and Nielson, 1969) range, 0.3 to 0.8.

Expected correlation between sire EBVs

Expected correlation between sire EBVs for an assumed genetic correlation of unity (r_G=1.0) is 0.63 (Table Two) which is higher than the mean observed correlation between EBVs of 0.11. Five percent of correlations between EBVs would be expected to have a value lower than 0.35 (P crit, P=0.05). Comparison-wise, none of the observed correlations between EBVs were less than 0.35, therefore significant (P=0.05) sire by environment interactions were detected for the traits analysed. There was sufficient evidence to reject the null hypothesis H_0: $r_G = 1.0$. If the true r_G was 0.3, the expected correlation between sire EBVs (0.18) would be closer to the average obtained in this study (0.11). Expected correlations between sire EBVs were likely lower in this study compared with previous studies due to low accuracy of sire evaluation or measurement differences between slaughter facilities.

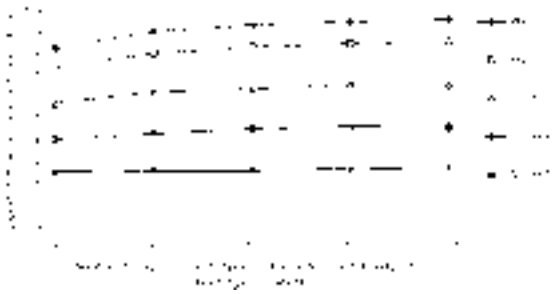
A lower than expected correlation between EBVs may result from presence of a true GxE interaction (r_G<1.0), differences in site and method of trait measurement or that sires were not chosen at random to enter the progeny test. Increasing progeny number evaluated per sire in each of two environments from 20 to 100 increased accuracy of breeding value estimation and mean correlation between sire EBVs from 0.68 to 0.93 (Figure One). Similarly, Notter and Diaz (1993) found that increased accuracy of evaluation of sires in both environments, decreased the number of sires required to reject the null hypothesis that r_G=1.0.

TABLE 2: Effect of genetic correlation between traits on expected correlation (using actual progeny numbers) between EBVs of sires evaluated from feedlot and pasture-finished progeny records.

True genetic correlation between traits	Expected (mean) correlation	P value (P<0.05)
r_G =1.0	0.63	0.35
r_G = 0.9	0.56	0.23
r_G = 0.7	0.44	0.06
r_G = 0.5	0.31	-0.11
r_G = 0.3	0.18	-0.27

Expected correlation between EBVs was sensitive to progeny distribution across environments, with 40 progeny per sire and assumed r_G of 1.0, (n_P = 20, n_F = 20) the expected correlation between EBVs was 0.83, however if (n_P = 10, n_F = 30), this expected value decreased to 0.79, the difference however was smaller as r_G decreased to 0.3, where for the same progeny ratios r_G became 0.26 and 0.24 respectively. The expected correlation between sire EBVs was 0.63 and 0.64 for 20 and 500 evaluated sires respectively.

FIGURE 1: Correlation between EBVs for two traits with differing genetic correlations and numbers of feedlot and pasture evaluated progeny.



If a genetic correlation of less than unity exists between true EBVs derived from pasture-finished and feedlot-finished progeny records and the majority of records are from feedlot-finished animals, omission of this genetic correlation will result in sub-optimal BV prediction when the goal of BV prediction is progeny performance in a pastoral environment (Notter, 1991). Therefore, unless r_G can be accurately determined from adequate progeny numbers (Robertson 1959, recommended 2000 half-sib progeny when h^2 = 0.25), EBVs should continue to be reported separately based on either feedlot or pasture-finished progeny records.

Assuming no selection of sires prior to entering the progeny test, the expected correlation between sire EBVs (for actual progeny numbers) was 0.63 decreasing to 0.45 when 14 sires were selected from 5000 available bulls ($\bar{i}$ = 3.0). Thus, failure to account for pre-selection of sires to enter the progeny test would over-estimate the expected correlation between sire EBVs. Intense selection pressure

for sires to enter the progeny test failed to result in expected correlation between sire EBVs close to observed values (0.45 vs. 0.11).

CONCLUSIONS

Correlations between sire EBVs were significantly (P>0.05) different from expected values for most traits analysed, providing evidence of sire by environment interaction based on progeny performance evaluated in pastoral and feedlot-finishing regimes. Further research with more sires and progeny per sire would more accurately determine if economically important GxE interactions exist between pasture and feedlot environments. If biologically and economically important sire by environment interactions are accurately determined, separate progeny testing programmes may be conducted in both pasture and feedlot-finishing environments.

ACKNOWLEDGMENTS

Funding for Breedplan research and extension support is provided by the New Zealand Meat Research and Development Council (MRDC). Data were provided from the Angus Carcass Evaluation and Progeny Test courtesy of Wrightson N.Z. Ltd. and the N.Z. Angus Association. Sincere thanks to Señor Nicolás López-Villalobos for assistance with simulations.

REFERENCES

Bertrand, J.K.; Berger, P.J.; Willham, R.L. 1985. Sire x environment interactions in beef cattle weaning weight field data. *Journal of Animal Science,* **60:** 1396-1402.

Bondoc, O.L.; Smith, C.H. 1993. The effects of genotype by environmental interactions in dairy cattle open nucleus breeding schemes. *Journal of Animal Breeding and Genetics, 110,* **3:** 186-193.

Buchanan, D.S.; Nielson, M.K. 1969. Sire by environmental interactions in beef cattle field data. *Journal of Animal Science,* **28:** 307-312.

Dickerson, G.E. 1962. Implications of genetic-environmental interaction in animal breeding. *Animal Production,* **4:** 47-63.

Falconer, D.S. 1952. The problem of environment and selection. *The American Naturalist,* **86:** 293-298.

Henderson. C.R. 1972. Sire evaluation and genetic trends. Proceedings of a Seminar held in honour of Dr. Jay L. Lush. Virginia Polytechnic and State University. 10-41.

Garrick, D.J.; Charteris, P.L.; Morris, S.T.; Purchas, R.J. 1994. Angus Carcass Evaluation and Progeny Test-Estimated Breeding Values. Department of Animal Science, Massey University, Palmerston North.

Hohenboken, W.D. 1986. Genotype by Environment Interaction. *In:* World Animal Science D, Animal Breeding and Genetics. Chapter 8: 151-163.

Notter, D.R. 1991. Accommodation of genotype x environment interactions in national genetic evaluation programs. *Proceedings of the 9th Conference of the Australian Association of Animal Breeding and Genetics:* 255-259.

Notter, D.R.; Diaz, C. 1993. Use of covariance's between predicted breeding values to assess the genetic correlation between expression of a trait in two environments. *Genetics, Selection and Evolution,* **25:** 353-372.

Robertson, A. 1959. The sampling variance of the genetic correlation coefficient. *Biometrics,* **15:** 469-485.

Van Vleck, L.D. 1994. Algorithms for simulation of animal models with multiple traits and with maternal and non-additive genetic effects. *Brazilian Journal of Genetics, 17,* **1:** 53-57.

Van Vleck, L.D.; Pollak, E.J.; Oltenacu, E.A.B. 1987. Prediction of additive genetic value from progeny records. *In:* Genetics for the Animal Sciences. W.H Freeman and Company, New York. 260-261.

Appendix One: Derivation of equation 1.

A matrix **V** of (co)variance between true and estimated breeding values can be represented as:

$$\mathbf{V} = \text{var}\begin{bmatrix} BV \\ EBV \end{bmatrix} = \begin{bmatrix} h^2 & h^2\, r_{TI}^2 \\ h^2\, r_{TI}^2 & h^2\, r_{TI}^2 \end{bmatrix} \sigma_p^2$$

This variance matrix, **V** can be decomposed into its Cholesky factors; **LL'** = **V**, where **L** is the lower triangular Cholesky decomposition of **V** (Van Vleck, 1994). A sample vector **s**, of variables from a population having variance **V**, can be simulated as **Lz** with **z** a vector of independent standardised random normal deviates (mean = 0, variance = 1).

$$\mathbf{L} = \begin{bmatrix} 1 & 0 \\ r_{TI}^2 & r_{TI}^2 - r_{TI}^4 \end{bmatrix} h\sigma_p^2$$

such that Lz comprises

$BV_i = h\sigma_p\, Z_i$

$EBV_i = r_{TI}^2\ BV_i Z_i + \quad r_{TI}^2 - r_{TI}^4 \quad h\sigma_p\, Z_i$

Given $h^2 = 0.25$ and $\sigma_p = 1.0$, for a progeny test with *n* offspring

then $r_{TI}^2 = \dfrac{n}{n+15}$ and $\quad r_{TI}^2 - r_{TI}^4 \quad h\sigma_p \dfrac{15n}{n+15}$

such that $EBV_i = BV_i \left[\dfrac{n}{n+15}\right] + \left[\dfrac{15n}{(n+15)}\right] Zi'$ as in [1] and [2]