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EFFECTIVENESS OF GROWTH PERFORMANCE SELECTION IN CATTLE

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SUMMARY

The effectiveness of performance selection or culling depends on the variability of the selection trait and its relationship with the economic measure of response. Progeny test information is necessary to evaluate and compare alternative selection methods.

The first experiment compared, over six years' progeny of 62 bulls selected for either fast or slow post-weaning gain in breeders' herds. Differences in progeny gains after weaning were small, reflecting a realized heritability of 0.16.

Six years' data were analyzed from a subsequent closed herd selection experiment and associated progeny test herd. Correlations among growth traits, both for individuals (within sires) and for progeny means, were high for liveweights themselves but lower for gains or between weights and gains. For 29 sires progeny-tested in two herds, the repeatability of tests was 0.36 for weaning and 0.43 for yearling weight. The regressions of progeny performance on sire's own performance, based on a total of 55 sires, are presented for different growth traits. Derived heritability estimates were of the order of 0.25 and 0.40 for weaning and yearling weight, but were small and non-significant for post-weaning gain.

The results are compared with overseas findings and discussed in relation to improvement of beef cattle growth performance. It is concluded that worthwhile genetic gains will be achieved by sire selection on yearling or weaning weight but *not* on weaning to yearling weight gain.

PERFORMANCE RECORDING has been widely advocated as a basis for selective improvement in beef cattle. Provided selection is for a trait or traits which are reasonably heritable, genetic theory asserts that effective progress can be made. Practical demonstration of the effectiveness of performance-based selection is however needed to check the validity of the theoretical predictions. Convincing demonstration could also provide a powerful stimulus to the wider adoption of performance testing.

The rate of genetic improvement through selection depends on the intensity of selection, the variability of the selection criterion and its genetic relationship with the measure of response, and the generation interval. Likewise, gains from culling depend on the proportion culled, the variability of the culling criterion and its phenotypic relationship with the subsequent measure of performance. Genetic and phenotypic associations between alternative criteria of selection and response clearly play a key role in determining the effective accuracy of selection and culling.

In the case of growth rate in beef cattle, performance can be measured either by weight at suitably chosen times or by weight gains over specified periods. Weights of animals at particular dates are known to be more sensitive to variation in age and other non-genetic influences, such as age of dam, than are weight gains over standard periods. Other things being equal, therefore, weight gains are likely to be more convenient practical criteria of selection or culling than are actual weights, particularly when birth dates and pedigree information needed for standardizing weights are not recorded.

Under New Zealand's seasonal grassland farming conditions, with cows calving in the spring and surplus beef animals slaughtered prior to their second winter at about 20 months of age, the most important liveweights in the assessment of growth are at birth, weaning, 14 months and 20 months. Birth weight is directly important through its influence on calving difficulty; it could also provide a useful aid to early selection (and particularly progeny-test selection) if in fact it were genetically associated with subsequent growth. Weaning weight is commonly regarded as an indicator of a dam's milking ability, although at normal weaning age its usefulness in this respect is limited. Its chief value is as a criterion for early screening or culling of bulls and heifers before their first winter feed shortage. Early mating, genetically desirable to speed up generation turnover, implies final selection of both males and females at about 14 months of age. Likewise, evaluation of growth performance of progeny to this age would permit selection and use of superior sires in the current breeding season. Liveweight at 20 months of age is the principal determinant of carcass weight and economic returns and hence is the most appropriate measure of response to selection. Mature size or liveweight is also economically important through its influence on maintenance requirements and consequently the calf production efficiency of the breeding cow, but will not be considered in this paper.

Numerous estimates of the important genetic parameters for beef production have been published over the past 25 years. Most are from American sources and based on paternal half-sib analyses of field or experimental data. It is assumed in such analyses that the sires represent a random sample of the male population and are mated to strictly comparable females. In practice some form of selection is usually applied in choice of sires themselves and the cows to which they are mated. Petty and Cartwright (1966) summarized estimates published up to 1965. The average heritabilities for weights and gains of pasture-fed animals up to 20 months of age are of the order of 0.30 to 0.40, with higher post-weaning values under feed-lot conditions. However, reported heritabilities, and to an even greater extent genetic correlations, show a very wide range of variation, reflecting not only large sampling errors but presumably also real differences between the populations studied in terms of both genetic and environmental components. Caution is clearly necessary in applying overseas estimates to New Zealand conditions.

The most accurate measure of the true breeding value of a bull for any trait is the average performance of a large number of progeny out of randomly-chosen dams. Except with wide usage of artificial breeding, however, progeny test selection has very limited value as a practical method of improvement, primarily because of the high proportion of cows within a breeding enterprise needed for the testing programme itself to ensure a high selection intensity. Under natural mating, rapid genetic improvement will be possible only if genetically superior sires can be effectively selected on the basis of their own performance. Progeny testing, however, provides the only sound basis for comparing the practical effectiveness of alternative selection methods.

This paper reports some provisional results on relationships among growth performance traits in beef bulls and their progeny from analysis of 12 years' progeny test records in the Waikeria experimental beef herd.

EXPERIMENT 1: PROGENY TEST COMPARISON OF FAST VERSUS SLOW GAINING SIRES

This project has been outlined by Brumby *et al.* (1963) in reporting some preliminary growth analyses.

For the first mating (calf drop 1957), five "fast" and five "slow" bulls were selected from 25 bulls brought to Ruakura as weaners from four studs, on the basis of weight gains from March (mean age 222 days) to the following December (mean age 488 days). In subsequent seasons bulls were chosen according to their weight gains from 9 to 21 months in their parent stud herds, each herd supplying one or more pairs ("fast" plus "slow") of bulls.

Initially bulls were mated to balanced groups of about 30 cows each, but subsequent replacement females were allocated within their own "line" (fast or slow). Heifers were first bred at two years of age until 1961, when yearling heifers were mated and the number of bulls increased from 10 to 12. Until 1961 calves were first identified, weighed, and males castrated at periodic marking dates. Calves were usually weaned in March (6 to 7 months of age) and all animals were weighed regularly. Steers were slaughtered at 1½ to 2½ years of age.

RESULTS

Since progeny birth dates were not obtained prior to 1961, comparison has been based on average daily gains together with age-corrected initial weights for sires and uncorrected final weights (18 to 21 months) for progeny. The mean differences for several performance traits between fast and slow bulls themselves and their respective progeny are summarized in Table 1. The results relate to a total of 62 sires with an average of 22 recorded progeny each.

TABLE 1: EXPERIMENT 1 — GROWTH DIFFERENCES,* FAST MINUS SLOW

Year[1]	*Sires*		*Progeny*		
	WW	*g*	*pg*	*g*	*FW*
1957	7	0.65	— 0.07	0.01	— 3
1958	23	0.86	0.07	0.14	63
1959	— 14	0.54	0.25	— 0.02	15
1960	34	0.49	0.10	0.10	70
1961	— 66	0.56	0.15	0.04	48
1962	2	0.53	0.26	0.01	63
1957-61	— 2	0.60	0.127	0.047	43

[1] Year progeny born.

*WW = Initial (weaning) weight (lb)

pg = pre-weaning average daily gain (marking to weaning).

g = post-weaning average daily gain (weaning to final weight).

FW = Final weight at 18 to 21 months (lb).

Averaged over all six years, the "fast" bulls showed an advantage over the "slow" in post-weaning daily gain of 0.60 lb per day. The corresponding difference in their progeny performance, 0.047 lb per day, was disappointingly small and accounted for approximately 20 lb difference in final weight. A surprising feature of the results, however, has been the consistent superiority, in all except the first year, of pre-weaning gains of the progeny of the "fast" versus "slow" sires. The average difference, 0.127 lb per day, accounted for a difference in weaning weight of 23 lb in favour of the "fast" progeny.

EXPERIMENT 2: COMPARISON OF SELECTION METHODS

To overcome the problem of properly assessing selection differentials for brought-in bulls, and as a basis for comparing alternative selection criteria, the preceding project was redesigned in 1962 to investigate beef cattle performance selection on a closed herd basis.

The experiment, still in progress, comprises closed selection herds on the one hand and a progeny-test herd on the other. Originally, three closed lines, each of 80 cows mated to three bulls annually, were established, selection being based, respectively, on corrected weaning weight, corrected final (October) weight, and weaning to October gain. In 1967 the weaning weight selection line was abandoned and the animals apportioned between the remaining two lines, each now of 125 cows mated annually to five bulls. All bulls in these herds are used as yearlings with selection based on growth rate information up to about 14 months of age. Replacement females are also mated as yearlings, cows being usually culled at 5½ years of age. Calves are weaned in February at about 5 months of age. Some culling of bulls is practised after weaning and again in early winter, non-selected animals being castrated. To control inbreeding, replacement heifers, selected on the same criterion as for bulls, usually remain in the sire sub-line in which they were bred, bulls being transferred between sub-lines.

To compare responses between selection lines, six two-year-old bulls each year of those previously mated as yearlings in the selection herds are progeny-tested in a separate test herd of 180 mixed-age cows. Male calves are castrated at or prior to weaning, and carried through to slaughter at 20 to 22 months of age. Heifer replacements are selected on the basis of their growth performance up to mating time at 14 to 15 months of age.

Results

For each calf drop 1963-69, and for the selection and test herds separately, a statistical covariance analysis was applied to the relevant progeny records. Sire constants (least squares progeny means) for each variable were estimated after allowing for the effects of sex, age, dam's age and other significant non-genetic factors such as grazing groups. Performance records on the sires themselves were adjusted using appropriate correction factors derived from these analyses. The residual (within sire) variances and covariances were pooled over years to form a single covariance matrix for each of the two sets of herds.

TABLE 2: TEST HERD, CALVES BORN 1964-69: SUMMARY*

Date		*Birth*	*Weaning*	*Sept.*	*Oct.*	*May*
Age (days)		—[1]	176	376	411	605
	M	68.6	420	570	642	885
Liveweight (lb)	F	64.4	387	520	552	
	M + F	66.4	403	543	595	
Regression	M	−0.13	2.2	2.1	1.9	1.6
on age	F	−0.12	1.8	1.8	1.7	
	M + F	−0.12	1.9	1.9	1.7	
	M	7.5	40.5	47.9	50.4	61.3
S.D.[2] (lb)	F	8.3	38.1	44.0	46.9	
	M + F	8.0	39.5	46.2	48.8	
CV[3]	M + F	12.1%	9.8%	8.5%	8.2%	6.9%

[1] Mean birth date Sept. 8; standard deviation 13.4 days.
[2] Residual standard deviation after eliminating regression on age.
[3] Coefficient of variation.
*Based on six calvings, 384 steers (M) and 427 females (F) except for May weights (five years and 313 steers only).

Means, regression coefficients and residual standard deviations from the pooled analysis of six years' progeny records in the test herd are summarized in Table 2. At all ages the steers were heavier than the heifers, although it should be noted that the sexes grazed separately after weaning. Except for birth weight, however, for which the females showed higher variability, coefficients of variation were closely similar for the two sexes, and declined steadily with age. Coefficients of variation were higher for weight gains (birth to weaning 11%, weaning to October 19%) than for liveweights themselves. Age differences accounted for 15 to 30% of the variation in liveweights at weaning and subsequently. The age-regression coefficients are higher for males than females and decline slowly with increasing age. Regressions of post-weaning gains on age are therefore negative but of small magnitude. A significant relationship exists between birth weight and birth date, later-born calves being heavier than those born earlier.

TABLE 3: TEST HERD 1964-9: CORRELATION (ABOVE DIAGONAL) AND REGRESSION* (BELOW DIAGONAL) COEFFICIENTS

Trait†	*BW*	*G(BW)*	*WW*	*G(WY)*	*YW*	*G(WF)*	*FW*
BW		0.23	0.42	0.08	0.40	0.12	0.33
G(BW)	1.07		0.98	−0.20	0.64	−0.05[n]	0.64
WW	2.07	1.05		−0.17	0.68	−0.02[n]	0.67
G(WY)	0.36	−0.20	−0.16		0.60	0.75	0.48
YW	2.43	0.85	0.84	0.81		0.49	0.87
G(WF)	0.75	−0.05[n]	−0.03[n]	0.95	0.43		0.73
FW	2.71	0.98	0.97	0.83	1.02	0.98	

[n] Coefficient not significant.
*Regression on preceding traits (top of column).
†Note: In this and following tables, BW, WW, YW, and FW denote weights at birth, weaning, yearling (Oct. for test herd, Sept. for selection herds) and 20 months (May). G ( ) denotes gain between the weights indicated.

Correlations between age-corrected growth traits on the same individuals are presented in Table 3. They are on a within-sire (paternal half-sib) basis but should approximate phenotypic correlations in normal herds. Birth weight is significantly correlated with later weights. The latter show very high correlations among themselves, implying useful prediction of later from earlier weights. Correlations among gains, or between weights and gains, are generally lower than those among weights. Weaning weight is negatively correlated with subsequent gains.

The influence of relationships among traits on gains from culling can best be inferred from study of the regressions of later on earlier traits, also shown in Table 3. On average, differences in birth weight are increased two- to three-fold in subsequent corrected liveweights, while differences in weaning weight are almost maintained at subsequent ages.

TABLE 4: STANDARD DEVIATIONS (S.D.) OF PROGENY TESTS AND CORRELATION (r) BETWEEN HERDS

	N^1	*BW*	*WW*	*G(WY)*	*YW*	*FW*
S.D. — Selection herds	55	3.4	14.6	15.7	22.5	
S.D. — Test herd	34[2]	2.3	12.8	11.0	17.3	29.7
r	29	0.31	0.36	0.36	0.43	

[1] Number of sires.
[2] 28 sires (five years) only for FW.

Sire constants, *i.e.*, corrected progeny means, estimated from the selection and test herds were themselves subjected to simple (unweighted) analysis of variance, eliminating differences between years. A total of 29 sires were progeny-tested in both herds. Standard deviations among sire constants for the different growth traits are presented in Table 4, together with the correlations between sire constants for the same traits in the two herds. The number of recorded progeny per sire averaged 18 and 24 for the selection and test herds, respectively. The correlations provide a measure of the repeatability of progeny tests which in turn reflects the heritability of the traits studied and the accuracy of the tests.* The significance of the correlations is reassuring.

Correlations between sire constants for the more important growth traits are summarized in Table 5 for the

TABLE 5: CORRELATIONS BETWEEN PROGENY TESTS FOR DIFFERENT TRAITS

Selection herds (6 years, 55 sires) above diagonal
Test herd (6 years, 34 sires*) below diagonal

Trait	*BW*	*WW*	*G(WY)*	*YW*
BW		0.58	— 0.04[n]	0.35
WW	0.50		0.10	0.72
G(WY)	— 0.02[n]	0.04[n]		0.76
YW	0.36	0.77	0.67	
FW	0.29	0.61	0.47	0.79

[n] Coefficient not significant.
*Five years, 28 sires only, for 20-month weights (FW).

*The approximate formula is: $r = nh^2/\{4 + (n-1)h^2\}$ where h^2 is the heritability and each test is assumed based on n progeny.

TABLE 6: REGRESSION OF PROGENY PERFORMANCE (SIRE CONSTANTS) ON SIRE'S OWN PERFORMANCE

Progeny Trait \ *Sire Trait*	*S.D.*[1]	*WW* *38.2*	*G(WY)* *42.8*	*YW* *39.1*
	BW	0.02^{n}	-0.01^{n}	0.01^{n}
Selection herds	WW	0.10	-0.01^{n}	0.08^{p}
(55 sires)	G(WY)	0.12	0.02^{n}	0.15
	YW	0.22	0.01^{n}	0.23
	BW	0.01^{n}	0.00^{n}	0.01^{p}
	WW	0.14	-0.04^{n}	0.10^{p}
Test herd	G(WY)	0.09^{p}	-0.01^{n}	0.07^{p}
(29 sires[2])	YW	0.23	-0.05^{n}	0.17
	FW	0.33	-0.14^{n}	0.30^{p}

[1] Within-year standard deviation, 55 sires.
[2] 23 sires only for FW.
^{n} Coefficient not significant.
^{p} Significant at 10% level.

two herds separately. All correlations among liveweights are significant; on the other hand, pre-weaning traits show little association with subsequent gain. Although these cannot be interpreted simply as genetic correlations, their environmental component is likely to be small suggesting significant genetic relationship between successive weights.

Comparative performance information was available on all (55) sires used in the selection herds including the (29) sires re-mated in the test herd. The regression coefficients, analysed on a within-year basis, of progeny performance (sire constants) for different traits on the sire's own performance for weaning weight, weaning to yearling gains and yearling (October) weight are presented in Table 6. Also tabulated are the standard deviations among sires within years for the three traits. The regressions represent the expected gain in progeny performance from a unit increase in the sire selection criteria. The significant relationships between progeny yearling or 20-month weights and the sire's own corrected weaning or yearling weight suggest that performance selection based on either of the latter traits should yield appreciable genetic gains. On the other hand, sire's gain from weaning to October is a very poor indicator of progeny performance for any of the traits listed and would appear useless as a selection criterion.

DISCUSSION

The small response achieved in Experiment 1 relative to the high apparent sire selection differential is perplexing and disturbing. The results in Table 1 imply a realized heritability of only 0.16 ($2 \times 0.047/0.60$) for post-weaning gain. It is possible that differential feeding could account for some of the difference in growth performance of the bulls themselves. In some contributing herds the so-called "top" bulls were treated preferentially and the selected "fast" sire would usually come from this group. This clearly underlines the importance of uniform management in any useful application of performance selection. Choice of bulls in the first year of the project could not be subject to this criticism since they were compared effectively in a central performance test. The disappointing results achieved dictate caution in the advocacy of similar performance test schemes. The results from Experiment 2 suggest that in fact post-weaning gain (at least up to 14 months) may be a very ineffective criterion of selection.

The apparent indirect response in terms of progeny pre-weaning gain may also in part reflect differential feeding levels. In some years the two "lines" were mated in different areas of the farm and evidence on cow weight gains over the mating period, which were closely associated with calf gains, suggests the "fast" groups may have been better fed than the "slow".

Two studies similar to Experiment 1 have been reported. Carter and Kincaid (1959) progeny-tested 19 pairs of sires, one selected for high, the other for low post-weaning feedlot gain, over a six year period. In terms of post-weaning daily gain, the sires differed by 0.59 lb per day, 177 steer progeny by 0.10 lb per day on feedlot and 192 heifer progeny by 0.06 lb per day on pasture. Heritabilities estimated from regression of progeny on sire were 0.21 for steers and 0.20 for heifers, compared with realized heritabilities of 0.34 and 0.20, respectively. Rollins *et al.* (1962) tested nine pairs of bulls similarly selected for fast or slow feedlot gain, with 5 to 10 steer progeny per bull. The sires differed on average by 0.37 lb gain per day. The "fast" progeny were 6 to 7 lb heavier at weaning but gained 0.03 lb per day *less* than the "slow" from 8 to 16 months.

In Experiment 2 the test herd should yield reliable progeny-test information. Cows are re-randomized among mating groups each year. This permits elimination of the effects of mating paddock differences on early calf growth, which have been shown (Carter, unpubl.) to account for up to 15% of the variation in weaning weights. By contrast, in the selection herds cows are not randomized between sires and mating groups remain unchanged, sire differences in calf performance being then confounded with possible mating paddock effects. In addition some sequential selection and castration of bulls is practised and the number of progeny per sire is less. The greater accuracy of progeny tests in the test herd is reflected in their lower standard deviations (Table 4).

The decline (Table 2) in coefficients of variation of liveweights from 13 months (8.5%) to 20 months (6.9%) parallels that found for pasture-fed dairy bulls (Carter, 1969), the coefficients dropping from 10.5% to 7.2% for Jerseys at similar ages. The standard deviations of birth weight (8.0) and weaning weight (39.5) agree well with corresponding average values of 8.1 and 45 reported by Petty and Cartwright (1966), bearing in mind the younger weaning age in the Waikeria herd.

The negative association between post-weaning gains and age or weaning weight reflects some degree of compensatory growth. In the case of age, however, it could be explained in part by the normal deceleration of growth rate. Detailed analysis of the data revealed that the effects of most environmental factors on weaning weight decrease only slowly for subsequent weights up to 20 months. This suggests that the addition of actual post-weaning gains to corrected weaning weights should provide a satisfactory measure of corrected later weights.

The correlations among age-adjusted weights and pre-weaning gains (Table 3) agree very closely indeed with the average phenotypic correlations reported by Petty and Cartwright (1966). On the other hand the negative relationships between post-weaning gains and pre-weaning gain or weaning weight contrast sharply with significant positive values from the U.S. studies. A possible explanation is the earlier weaning age in the present data. Average genetic correlations among traits (Petty and Cartwright, 1966) are positive and substantially higher than corresponding correlations among sire constants in this study (Table 5), except for those between weaning weight and birth weight (0.58) or yearling weight (0.79) which are similar. Nevertheless the magnitude of the correlations among weights suggests that sires will rank quite similarly for progeny-test performance on weaning and subsequent weights, justifying provisional selection at the weaning or yearling stage. Progeny birth weight itself appears to have useful predictive value in this respect.

Gains from selection or culling depend on the variability of the selection criterion as well as its relationship with subsequent response. From the values presented (Tables, 2, 3, 6) it can be inferred that, in improving final weight, age-corrected liveweight at the end of a test period is a better selection or culling criterion than preceding weight gain. Likewise, selection of sires on yearling weight should yield about 15% greater genetic response in either yearling or 20-month weight than will selection on weaning weight.

The heritability of a trait can be estimated as twice the regression of progeny performance on sire performance. Appropriate estimates with their standard errors derived from Table 6 for the test herd (selection herds in parentheses) are 0.29 ± 0.13 (0.20 ± 0.11) for weaning weight and 0.35 ± 0.19 (0.45 ± 0.15) for yearling weight. Values for post-weaning gain do not differ significantly from zero. The estimates could be biased (Carter, unpubl.) by the effect of selection of sires; it will be noted that the standard deviation among sires for yearling weight (39.1) is substantially less than that for a random group of steers (50.4) — see Table 2.

Very few large-scale studies relating progeny to sire performance have been reported. The results of Carter and Kincaid (1959) have already been discussed. Koch and Clark (1955) obtained correlations among birth weight, pre-weaning gain and weaning weight between 85 sires and their progeny, deriving a heritability value of 0.25 for weaning weight. Lessells and Francis (1968) tested 39 performance-recorded Hereford bulls on Friesian cows, progeny being reared at two locations. Although significant correlations were established between daily gains from birth of sires and their progeny (heritability 0.42), the authors concluded that selection of sires on their average daily gain would result in little genetic improvement because of the small variation in this trait.

The main conclusion emerging from the present results is that considerable scope does exist for improving progeny growth performance by selecting bulls on their own corrected liveweights but *not* on post-weaning gain, at least up to 14 months of age. Information is clearly needed on the relative merits of post-weaning gain over a longer period and of liveweights at older ages as selection criteria. The importance of adequate correction of growth performance traits for non-genetic sources of variation must be emphasized.

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