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Selecting on pubertal traits to increase beef cow reproduction

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ABSTRACT

An experiment was established at Waikeria, near Te Awamutu, to select for pubertal traits in Angus cattle, with selection first applied to the animals born in 1982. The aims of this paper are to report on genetic parameters for age at first oestrus (AFO) in heifers, weight at first oestrus (WFO) in heifers, scrotal circumference (SC), 13-month weight (W13) and calving day (CD), to compare the performance of young animals in the selection and control herds, and to assess prospects of achieving a correlated response in calving rate. Three selection herds and a control were set up, with single selection objectives being SC, AGE+ and AGE-, where '+' and '-' indicate selection for greater or lesser AFO. Phenotypic coefficients of variation were 15% for AFO, 11% for WFO, 8% for SC, and 8% for W13. Corresponding heritability estimates from Waikeria were 0.15, 0.30, 0.24 and 0.33, compared with those from other New Zealand research herds which averaged 0.34, 0.37, 0.38 and 0.36 respectively. The genetic correlation estimate for AFO and SC was -0.81 ± 0.38 , with -0.50 ± 0.29 for standardised AFO and SC. The response in AFO up to the 1991 calf crop was 16.5 d between the AGE+ and AGE- herds, a small divergence of 4.3% so far, because of selection within one sex only. From 1992, index selection has been applied in both sexes. The direct response in SC up to 1991 was 1.6 cm or 5.3% above the control.

Using information on relatives and correlated trait information to estimate breeding values for the sex which is not measured, potential annual single-trait responses for AFO are 0.96% and for SC 0.94%, assuming a genetic correlation of -0.4 between AFO and SC. These are respectively 68% and 19% greater than the potential responses to individual selection in one sex. The limited number of literature estimates for beef cattle suggest that cow lifetime reproduction should respond to selection for pubertal traits (reduced AFO or increased SC).

Keywords: Cattle, Angus, pubertal-age, scrotal circumference, genetic parameters.

INTRODUCTION

Background: Concept of the genetic correlation between sexes

Land (1973) was the first to suggest a likely genetic correlation between the reproductive characters of mammalian males and females, based on underlying hormonal relationships common to both sexes. His test of the hypothesis was carried out in mice (Islam *et al.*, 1976). Land *et al.* (1980) reviewed eight experiments in mice, pigs or sheep on genetic associations between testis size and ovulation rate; with two exceptions in sheep, all other experiments showed positive associations for these traits, both between and within populations. In beef cattle, previous New Zealand estimates of heritabilities for pubertal traits in males and females are shown in Table 1, along with the genetic correlations estimated between them. The female pubertal trait recorded has been age at first oestrus (AFO), for which a value below the mean shows advanced puberty; for puberty in males, precocious animals have a large scrotal circumference (SC). Therefore, the negative genetic correlations in Table 1 are consistent with Land's (1973) theory, although the estimates of Parratt *et al.* (1987) were expected to be less precise than those of Morris *et al.* (1992a) because of fewer sire groups.

The data described by Parratt *et al.* (1987) came from an experiment with Angus cattle, which was established to investigate and eventually exploit genetic variation and covariation

TABLE 1: Previous estimates of genetic parameters for pubertal traits in New Zealand beef cattle

Authors ¹	No. of sires	Heritability			Genetic correlation			
		AFO ²	SFO	WFO	SC	AFO,SC	SFO,SC	WFO,SC
1.	70	0.36	0.38		0.50	-0.07	-0.02	
2.	234	0.33	0.32	0.40	0.29	-0.39	-0.19	-0.39
3.	63				0.36			
4.	161	0.34	0.49	0.34				
Average		0.34	0.40	0.37	0.38	-0.23	-0.11	-0.39

¹ 1 = Parratt *et al.* (1987), 2 to 4 = Morris *et al.* (1992a, 1992b, 1993) respectively.

² AFO = age at first oestrus; SFO = standardised age at first oestrus; WFO = weight at first oestrus; SC = scrotal circumference.

in pubertal traits. There is no other published beef cattle experiment known to us where selection has been applied to pubertal traits. Experimental details are given below, but the ultimate goal is to expand Land's (1973) concept of the underlying hormonal relationships which are common to both sexes, to look across ages. Little is published in cattle on genetic correlations between cow or bull reproduction traits and pubertal traits measured in either sex. The bull reproductive traits that are relevant include fertility, non-return rate in mates, serving capacity and breeding soundness score, while for cows they include average calving rate (CR), longevity

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and also calving day (CD). Ponzoni (1992) has contrasted the importance of genetic change in CR versus CD; his calculations have shown that (at least under assumptions of a normal distribution for CD, with a standard deviation of 20 days), a 1-day earlier conception date (if translated into a 1-day earlier CD) is equivalent to a 1% increase in herd CR.

Genetic correlations between pubertal traits and adult cow reproduction

The most convincing evidence of a favourable genetic relationship between male and female reproductive traits in cattle comes from Mackinnon *et al.* (1990a), who estimated responses in males at CSIRO Lansdown (Queensland) from herds where selection was for high or low CR in cows. A 12% difference in CR in the mixed-aged cow herds was positively associated with a 1.0 cm difference in SC in bulls at 12 months of age ($P < 0.10$) and a 1.6 cm difference in SC at 18 months ($P < 0.05$). CR in heifers in the two herds also differed by 12% ($P < 0.05$), in spite of similar live weights in each herd at mating; circumstantial evidence suggested that there had been accelerated sexual maturity in high line bulls and heifers, relative to low line animals.

In Danish dairy cattle, Janson (1980) found large positive genetic correlations between heifer and 2-year-old cow CR, as for heifers and cows at CSIRO Lansdown.

Meyer *et al.* (1991) calculated genetic correlations between SC and days to calving (analogous to CD), from three batches of Australian data consisting of Angus, Hereford and Zebu-cross herds. The correlation estimates were all negative and averaged -0.30.

In South Africa, Swanepoel *et al.* (1992) classified a herd of Bonsmara cows with lifetime calving records into those which averaged phenotypically short or long calving intervals. The sons of those with short calving intervals had greater SC at 12 and 15 months of age ($P < 0.05$) than the sons of those with long calving intervals.

In the USA, Brinks *et al.* (1978) were the first to study correlations across sexes in beef cattle. Results reported later from the same group (Smith *et al.*, 1989) described reproductive data from daughter groups sired by 60 bulls measured for SC, using inbred lines of Hereford, Angus and Red Angus cattle. Regressions of daughter performance on sire's SC were not significant but were generally favourable in sign, as follows, -0.80 d/cm for AFO, -0.83 d/cm for age at first calving, -0.67 d/cm for date at first calving and +0.60 d/cm for date at second calving. Toelle and Robison (1985) reported genetic correlations with yearling SC from 63 paternal half-sib groups of Hereford heifers as follows (with sire-daughter genetic correlations in brackets), -0.14 (0.58) for age at first calving, 0.56 (0.93) for yearling heifer pregnancy rate and -0.42 (0.20) for the intercalving interval from 2 to 3 years of age. The variability in sign between results from these two groups of authors, and within the data of Toelle and Robison (1985) suggest that more data are needed to improve precision for these pairs of traits.

Theoretical calculations have also been carried out into responses in adult CR following selection for SC (Hammond and Graser, 1987). For example, assuming that CR has a heritability of 0.05, they calculated in their Table 3 that CR

should respond by 0.1% per year to SC selection when the genetic correlation between CR and SC is 0.1 and by 0.2% per year when the genetic correlation is 0.2. Similar calculations can be done for CR in response to selection for AFO, and the Ponzoni (1992) theory implies that any correlated responses in CD are also relevant.

Genetic correlations of adult reproduction traits between sexes

Mackinnon *et al.* (1990b) have reported genetic correlations among reproductive traits within 6 purebred and crossbred herds at CSIRO Rockhampton. From analyses of 16 514 mating records, comprising cows from 542 daughter groups, they estimated a positive genetic correlation between bull and cow fertility (0.16). This was consistent in sign with an estimate of the same parameter by Bamualim *et al.* (1984) of 0.33, from the CSIRO Lansdown experiment mentioned earlier. There were no significant differences between the two Lansdown herds in CD (Hetzl *et al.*, 1989).

In dairy cattle, Hansen (1979) obtained three genetic correlation estimates averaging -0.15 between bull fertility and intercalving interval in cows. Syrstad (1983) published genetic correlation estimates for non-return rates for bulls and cows in Norway; combining his result with a second (but unpublished) Norwegian estimate gave a value of 0.14 ($P < 0.01$).

The New Zealand experiment

An experiment was established at Waikeria, near Te Awamutu, to select for pubertal traits in Angus cattle, and to monitor correlated responses in adult reproduction. Because the foundation stock consisted of selected herds, a generation of crossing had to precede the new selection work, providing data for the parameter estimates published by Parratt *et al.* (1987). A total of 141 sires have been used since puberty selection began, now providing sufficient data for further genetic parameter estimates on pubertal traits, although not on cow reproductive traits. The first aim of this paper is to report on genetic parameters from the Waikeria herd for AFO in heifers, weight at first oestrus (WFO) in heifers, SC in bulls, 13-month weight (W13) in both sexes and CD, in relation to estimates from other New Zealand herds. The second aim is to compare early selection responses, from the performance of young animals in the control and selection herds.

MATERIALS AND METHODS

Herd definitions

Foundation stock at Waikeria resulted from first crosses among two herds selected for weight or weight gain and a progeny testing herd managed on the same property from 1964-81 (Carter *et al.*, 1990). Three selection herds were established from the gene pool derived from these first crosses, beginning with the animals born in 1982. The first herd (SC) was selected for increased scrotal circumference using phenotypic selection in males, and random selection of

yearling heifer replacements. The second herd (AGE-) was selected for reduced AFO in heifers using phenotypic selection for AFO, but phenotypic selection in bulls was for increased W13 adjusted for age of dam and date of birth. The third herd (AGE+) was selected for increased AFO in heifers using phenotypic selection for AFO, and again phenotypic selection in bulls was for increased adjusted W13. A transformation was applied to the AFO variate for selection purposes (as described later), with retrospective selection applied to heifers after the end of joining, at 18 months of age. Foundation mixed-aged cows (born in 1975-81) were randomised to the three selection herds at the time of the 1984 matings. A Control cow herd was established from a random sample of animals born in 1982 and subsequently, from the same gene pool of first crosses described above. During this establishment period, animals were not transferred between herds, once originally allocated.

Single-trait selection within sex was continued from the 1982 calf crop for 9 years up to the 1990 calf crop inclusive, after which best linear unbiased prediction (BLUP) procedures were introduced to select bulls and heifers for the transformed AFO variate in the two AGE herds, using AFO and SC records.

For the calf crops born in 1985-91, reported here, a total of 141 different sire groups were represented, consisting of a panel of 37 Control bulls used repeatedly over years by artificial insemination (AI), and 104 bulls used in the selection herds. (For traits where records were only available up to the 1990 calf crop, corresponding figures were 126 sires, comprising 37 controls and 89 selected bulls).

Herd management and recording

A total of about 550 cows and yearling heifers were mated each year, with 400 to 450 pregnant animals wintered, comprising about 90 Controls and 120 selection animals wintered in each herd. Females were single-sire mated (without oestrous synchronisation), using natural mating for about 7 weeks in the selection herds (5 yearling bulls per herd). AI in the Control herd was carried out (again without synchronised oestrus) over the same time period as matings in the selection herds, using a panel of semen collected and stored at the beginning of the experiment (1 son per sire, from 37 sons born in 1982-84).

Apart from the mating period, cow herds were grazed together in large management groups, with hay supplementation (but no concentrates) in winter. Calves were all weaned on one day at about 6 months of age. Heifers were then run in one management group until the start of mating at an average of 14 months of age, while bulls were generally randomised into 2 or 3 groups and grazed until October (13 months of age). Calves also received some hay supplementation (but no concentrates) in winter.

Calves were identified to dam and weighed at birth, at 2 months of age (when their dams were reallocated for mating), at weaning and then regularly (every 4 to 6 weeks) until 13 months of age. Heifers were recorded for date at puberty by observing paint marks from vasectomised bulls fitted with chinball harnesses (and, from this, AFO was calculated and WFO was interpolated using the regular weight

data). The SC in bulls was recorded with a tape measure at 9, 11 and 13 months of age.

All heifers were joined, and heifer selection was made retrospectively at the time of pregnancy diagnosis in March/April, using AFO data obtained before and during mating. Cows were also pregnancy tested, and non-pregnant heifers and cows were culled.

Statistical Methods

The least squares analysis of variance computer programme was used (Genstat, 1990) to establish appropriate statistical models for fixed effects. Restricted maximum likelihood (REML) procedures (Patterson and Thompson, 1971) were then used to compare herd x year combinations at the same time as obtaining heritability estimates for AFO, WFO and W13. Fixed effects included herd, year of birth, herd x year interaction, age of dam, sex of calf (for live weights), and a covariate for date of birth. For SC where 3 records were available for each animal, repeatability and heritability estimates were obtained simultaneously. Additional fixed effects were necessary for SC, to adjust for record number, and nesting record number within year. For SC and W13, where animals were subdivided into management groups, year-management groups were coded instead of 'years'. In the same way, the repeatability and heritability REML model was used to analyse CD treated as a cow trait (calvings 1987 to 1992, including cow ages 2 to 7 years).

Data for AFO were analysed both with and without a transformation. The original scale was transformed to an underlying scale with a standard deviation of unity, as if AFO was an ordered categorical response, but including animals which had not shown an oestrus (Gianola and Norton, 1981). This trait was referred to as standardised age at first oestrus (SFO), and it was analysed using fixed effects and mixed models in the same way as AFO.

Genetic correlations were obtained using the BIREML programme of Meyer (1986), accounting for half-sib groups of the two sexes being managed separately.

In addition to any genetic correlations with SC, bulls with a larger SC may have the opportunity to get more cows in calf (or to get more cows pregnant early in the season) than contemporary bulls. A preliminary investigation was undertaken for the three selection herds (i.e. excluding the control herd which used AI), with matings in 1986-91 and subsequent calvings in 1987-92. In total, 89 bulls or mating groups (71 degrees of freedom) were involved, and the regression of the mean CD of cows in a bull's mating group on his own SC was estimated after adjustment for herd x year of calving, calf sex and age of cow. All bulls were used once only as yearlings.

RESULTS

Environmental effects

Table 2 shows the environmental effects for pubertal traits, W13 and CD. Heifers from 5-year-old dams were younger but heavier at puberty, and bull calves had larger SC, than those from 2-year-old dams, whilst CD was not significantly different.

TABLE 2: Phenotypic standard deviation, heritability and effects of fixed factors on pubertal traits¹, 13-month weight and calving day

Parameter	AFO,	SFO	WFO,	SC,	W13, kg		CD,	
	d		kg	cm	F ²	M ²	d	
Overall mean	362	0.03	274	30.8	295	321	241	
Number of animals	959	1006	960	1190 ³	946	951	575 ³	
Phenotypic SD	52.9	0.97	31.3	2.5	21.9	29.4	12.2	
Coefficient of variation, %	14.6	-	11.4	8.1	7.4	9.2	5.1	
Heritability	- estimate	0.15	0.23	0.30	0.24	0.37	0.29	0.05
	- SE	0.09	0.10	0.11	0.08	0.11	0.11	0.07
Regression on date of birth (per d)								
	- estimate	0.48	0.0039	-0.052	-0.071	-0.81	-1.20	-
	- SE	0.14	0.0025	0.082	0.005	0.06	0.08	
Effect of age of dam (5-yr-old minus 2-yr-old)								
	- estimate	-27.2	-0.47	7.9	1.8	22.5	24.8	0.6 ⁴
	- SE	5.1	0.09	3.0	0.2	2.0	2.7	1.2

¹ Abbreviations for pubertal traits are described in Table 1; W13 = 13-month weight; CD = calving day; SC and CD were treated as repeated traits.

² F = females; M = males.

³ Mean SC = 27.0 cm (June), 31.3 cm (August), 34.1 cm (October); 3 SC records per animal; repeatability of SC among recording dates = 0.74±0.01. For CD (mean 2.50 records per animal), repeatability = 0.16±0.03. Standard deviations for SC and CD are for an individual record, rather than for the mean for each animal.

⁴ The fixed effect for CD is age of cow.

Regressions on date of birth were not significantly different from zero for WFO or SFO. However, late-born heifers had greater AFO than early-born heifers ($P < 0.01$), if comparisons were made using this truncated trait. Late-born bulls had significantly smaller SC ($P < 0.01$) than early-born bulls. Coefficients of variation were 15% for AFO, 11% for WFO, 8% for an individual record of SC and 8% for W13. For CD, the coefficient of variation was 5.1%, but was dependent on the season of calving chosen; the standard deviation was 12 days. Repeatabilities were high (0.74±0.01) for SC, but low (0.16±0.03) for CD.

Genetic Parameters

Table 2 also shows the heritability estimates for the pubertal traits and W13 and CD. Values for SFO, WFO, SC and W13 were of moderate size, whilst those for AFO and CD were small. The estimates for SC and CD represented the values for individual records, rather than for the mean of all data recorded on each animal.

Table 3 shows the estimates of genetic correlations between male and female traits. AFO and SFO had negative genetic correlations with all three male traits shown (average SC being from 3 records per bull), whilst genetic correlations with WFO were negative for SC and positive (though small) for W13 in males. The values for W13 in females with 13-month or average SC were small and non-significant, whilst the value for W13 in females and W13 in males was 0.51. Genetic correlations with 3-year-old CD were very small; estimates were not obtained for 2-year-old CD as there was a bias for this trait because late pubertal heifers had little or no opportunity to get pregnant.

The phenotypic regression of the mean CD of cows in a bull's mating group on his unadjusted SC was -0.54 ± 0.16 days/cm ($P < 0.001$), indicating that (other factors being equal) a 5-cm or 2 phenotypic standard deviation increase in SC in yearling bulls should lead to a 2.7-day earlier mean CD.

TABLE 3: Genetic correlations¹ between measures of performance² in females and males (105 sire groups)

Female trait	13-month SC	Male trait	W13
		Average SC	
AFO	-0.81(0.38)	-0.64(0.36)	-0.41(0.37)
SFO	-0.50(0.29)	-0.40(0.29)	-0.28(0.29)
WFO	-0.43(0.26)	-0.45(0.25)	0.19(0.27)
W13	0.11(0.26)	-0.06(0.25)	0.51(0.24)
CD (3-yr-old) ³	0.02(0.35)	-0.05(0.36)	0.12(0.38)

¹ Standard errors in brackets.

² Abbreviations for traits are described in Tables 1 and 2; average SC = average of records at 9, 11 and 13 months of age.

³ Estimates were not obtained for 2-year-old CD.

Selection and Control Herds

Table 4 shows the means of the Control herd for each trait, and the contrasts between the SC and Control herds, and between the AGE+ and AGE- herds, for the last 2 years of records available. The SC herd was younger in AFO by 21.3 days in the final 2 years than the Control. The difference of 16.5 days in AFO between the AGE+ and AGE- herds was only 77% of the SC response in the most recent 2 years. Corresponding estimates for SFO were consistent with those for AFO, given a standard deviation of 53 days. For each herd, correlated responses in WFO were in the same direction as changes in AFO, with larger differences in WFO being found between the AGE herds than between the SC and Control herds. Responses in SC were 1.6 cm in the SC herd, with no difference between the AGE- and AGE+ herds. For the data collected in the experiment so far, interpreting CD is complicated because AI was used in the Control herd, while natural mating was used in the selection herds. The difference in CD between AGE+ and AGE- herds however was not significant.

TABLE 4: Effects¹ of selection herds and control herd² on pubertal traits, 13-month weight and calving day

Trait ³	Control mean	SC herd minus Control	AGE+ minus AGE-	Average SE of herd differences
AFO, d	386	-21.3	16.5	9.7
SFO	0.31	-0.36	0.33	0.18
WFO, kg	286	-2.2	12.3	6.2
SC, cm	30.3	1.6	0.1	0.6
W13, kg	282	6.5	4.9	5.9
CD, d	244	-4.6 ⁴	0.5	1.6

¹ Most recent two years: calf crops born in 1989 and 1990 for heifer puberty traits; calf crops born in 1990 and 1991 for scrotal circumference and 13-month weight; calvings in 1991 and 1992 for calving day.

² SC = scrotal circumference herd

AGE+ = herd selected for increased age at puberty in heifers

AGE- = herd selected for reduced age at puberty in heifers

³ Abbreviations for traits are described in Tables 1 and 2.

⁴ Interpretation complicated by artificial insemination in the Control herd

DISCUSSION

Parameter estimates from Waikeria

Previous genetic parameter estimates for pubertal traits in New Zealand were summarised in Table 1. The heritability estimates averaged 0.34 for AFO, 0.40 for SFO, 0.37 for WFO and 0.38 for SC, compared with the somewhat lower values here of 0.15, 0.23, 0.30 and 0.24 respectively. The estimates from this study could however be biased downwards by selection effects.

Morris *et al.* (1992a) obtained a repeatability estimate for SC at 8, 11 and 13 months of age of 0.42 ± 0.02 (from a harsher environment), compared with a value of 0.74 ± 0.01 here. The heritability and repeatability estimates for CD were found by Morris *et al.* (1987) from 57 sire groups to be 0.05 and 0.19, and by Morris *et al.* (1993) from 161 sire groups to be 0.02 and 0.10 respectively, compared with 0.05 and 0.16 here.

The genetic correlations of SC with female pubertal traits in Table 1 can be compared with -0.81 for SC with AFO here, -0.50 with SFO and -0.43 with WFO. Although estimates all had large standard errors, the important point was that all had a negative sign.

For the phenotypic regression of average CD of cows in a bull's mating group on his own SC (-0.54 ± 0.16 days/cm), there are no other published New Zealand estimates. For comparison, we estimated the regression from the females at Goudies whose puberty data were reported by Morris *et al.* (1992a) and for which calving data (as a result of an 8-week mating period) were subsequently recorded. For cows calving in 1982-87 as a result of conceiving in 138 yearling-bull mating groups (91 degrees of freedom, after fitting breed x year of calving), the regression of CD on SC was 0.10 ± 0.17 days/cm. Thus, there seemed to be no consistency between the two batches of data.

Selection responses achieved

At this early stage in the selection programme, SC has

responded in the SC herd (relative to the Control), but there was no difference in SC between the AGE+ and AGE- herds. AFO and SFO have responded to direct selection in the AGE herds and to indirect selection in the SC herd. WFO and W13 did not change significantly in the SC herd, and the interpretation of any weight responses in the AGE herds is complicated by the fact that positive weight selection was applied to bulls in both of the AGE herds. CD did not change significantly in the AGE herds. The puberty results were consistent with the genetic correlation estimates (Table 3) and were consistent with large negative between-breed correlations for AFO and SC reported in New Zealand by Morris *et al.* (1992a) and in the USA by Gregory *et al.* (1991). The latter authors found only minimal correlation between WFO and SC.

From two generations of progress in the present experiment, selection within females only has so far achieved a 16.5 day (0.31 SD units or 4.3%) divergence in AFO, whilst direct selection for SC has increased SC relative to the control by 1.6 cm (0.64 SD units or 5.3%). From the progeny of the 1991-born bull calf crop onwards, (i.e. selection applied in 1992), the selection response for SFO should increase as a result of introducing multi-trait BLUP procedures with SFO and SC.

Theoretical responses

Expected responses to single-trait selection were calculated for AFO and SC, assuming phenotypic standard deviations of 53 d and 2.5 cm, and heritabilities of 0.30 for both (given the estimates in Table 2 and the larger literature values). Comparisons were also made with single-trait selection for WFO in females (phenotypic standard deviation 31 kg, heritability 0.33) or for W13 in both sexes (phenotypic standard deviation 26 kg, heritability 0.35). The generation interval was 3.1 yr, and selection intensities were 2.0 and 0.8 in males and females respectively. Individual selection is expected to change AFO or WFO by 0.57% or 0.48% per year respectively (female selection only), SC by 0.79% per year (male selection only) and W13 by 1.33% per year (selection in both sexes). The different coefficients of variation, e.g. for AFO (14.6%) and SC (8.1%), and different selection intensities accounted for the contrasting results. Including 10 paternal half sibs of the same sex is expected to increase responses slightly. However, combined selection for AFO using AFO records from the individual and 10 paternal half sisters, along with 10 paternal half brothers' records of SC was also tried, assuming a genetic correlation of -0.4. Selecting for reduced AFO would give an expected response of 0.96% per year, whereas the converse selection for greater SC using both sexes would give an expected increase of 0.94% per year. Thus, combined selection for AFO or SC is expected to be respectively 68% and 19% superior to individual selection in one sex.

CONCLUSIONS

Responses to direct selection for pubertal traits will continue to be monitored, and the correlated traits of adult reproduction should be measured in the future. The limited

data available from the literature on relationships between cow lifetime fertility and puberty mostly show that the traits are favourably correlated, as has also been found in other mammalian species.

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