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Responses to selection for pubertal traits in Angus cattle over 23 years

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ABSTRACT

Selection to change age at puberty over 23 years was monitored in Angus cattle in a Ruakura study. A foundation herd was divided in 1984 into four lines: a control unselected line, and lines selected for high age-at-puberty (Age+), low age-at-puberty (Age-), and high scrotal circumference (SC), with the last two lines being merged later. Age at puberty (first oestrus, AFO) was determined in heifers from observations of first behavioural oestrus date; puberty was determined in bulls from SC records from 8 to 13 months of age. Selection for AFO was applied mainly to bulls, using the genetic correlation between AFO and SC from our data (-0.25 ± 0.09). Puberty records from 6,473 weaned calves were analysed, using restricted maximum likelihood methods to determine genetic changes achieved by line. Realised heritability estimates were 0.26 ± 0.03 (standardised AFO), and 0.40 ± 0.04 (individual SC records; repeatability over ages, 0.68 ± 0.01). Averaging over recent year's data, Age- line heifers had lower AFO than Age+ line heifers by 69 days (19%; 1.33 phenotypic standard deviations), and bulls had larger SC by 3.0 cm (9.9%; 1.17 phenotypic standard deviations). Correlated responses in pregnancy rate favoured Age- over Age+ females at all ages.

Keywords: cattle; puberty; breeding; selection; oestrous age.

INTRODUCTION

Puberty traits in beef cattle are known to be heritable under grazing conditions (Morris *et al*., 1992; 1993), as well as under more intensive conditions (Splan *et al*., 1998). Age at puberty (AP) and weight at puberty (WP) are both important as target traits in beef production situations when there is very limited feed supply and slow growth rates over extended periods, although this seldom applies in New Zealand. However, studying the genetics of pubertal traits, especially any genetic correlation with later reproductive performance, should provide an understanding of early indicator traits needed to breed for increased reproduction. The aim of this study was to manage a long-term selection experiment with single-suckled Angus calves, to breed two lines diverging in heifer AP. As far as we know, AgResearch has carried out the only multi-generation experiment with AP selection in cattle. We report here the direct responses in heifer AP and the male pubertal trait, scrotal circumference (SC), relative to an unselected contemporary Control line that was maintained alongside the selection lines for the first 18 years. The experiment was managed for 23 years, being terminated after six generations of selection.

MATERIALS AND METHODS

Ethics

This experiment was carried out using a trial design approved by the Ruakura Animal Ethics Committee (currently AEC 11431).

Animals

Early phases of the puberty selection experiment were described in a previous Conference paper (Morris & Wilson, 1997). Briefly, the foundation Angus stock in 1984/85 came from a prior experiment (calvings 1964 to 1981) where lines had been selected for weight or weight-gain traits (Carter *et al*., 1990), followed by three years of re-randomisation by line crossing (calvings 1982 to 1984). Alongside an unselected Control line, three puberty lines were then reorganised in 1984/85, to calve from 1985, and selected for increased AP in heifers (Age+ line), reduced AP in heifers (Age- line), or increased SC as a predictor of AP in female relatives (Land, 1973). The Age- and SC lines were merged from the 1992 matings, forming a new Age- line, with continued selection applied for reduced AP in heifers.

The lines were grazed on pastures which were predominantly a mix of ryegrass and white clover, with some supplementation of silage or hay in periods of feed shortage. No concentrates were fed. All lines grazed together except at single-sire mating time. Mating began at the same time each year, lasting for an eight week period in all lines of breeding females, including yearling heifers, with chinball-harnessed selection-line bulls. Artificial insemination was used in the Control line for the first eight years, using a semen panel of 37 bulls bred before the puberty selection began, and natural mating thereafter. Each selected or Control sire was joined with an age-balanced sample of females from his own line, except in 1999 to 2002 when back-cross calves were also generated. Generally four to five bulls were mated per line. About 120 to 150 cows and heifers were joined per line each year until 1991, with modified numbers from 1992 onwards. There were approximately 160 per year in the Age-line, 60 to 90 in the Control line, and 70 to 120 in the Age+ line. The herd was managed at the Department of Corrections, Waikeria Farm, Te Awamutu, until September 1992, transferred to AgResearch's neighbouring Tokanui Station near Te Awamutu for 14 years, and then transferred to AgResearch's Whatawhata Research Centre (west of Hamilton) in June 2006, where it continued for a further two years. This encompassed six generations since commencing the trial.

Stock management and recording

Calves were tagged and identified to dam within 24 hours of birth. The definition of AP for heifers in the study was the date, and hence the age, of first behavioural oestrus (AFO). Oestrus was monitored by staff about twice-weekly in heifers from 8 to 17 months of age, with the assistance of paint marks from chinball-harnessed vasectomised bulls. During the mating period from 14 to 16 months of age, entire bulls were used, sometimes with the use of tailpaint. SC was measured with a flexible tape on all bulls every month, from 8 to 13 months of age. Cow and calf weights were recorded routinely. Cow culling was predominantly on non-pregnant animals, three years-old or more, and on chronological age. Generally all yearling heifers were retained for joining, and non-pregnant yearlings were given a chance in a second mating season if necessary to avoid confounding late puberty with a low lifetime survival age resulting from non-pregnancy.

Data analysis

A total of 6,473 weaned calves were recorded for AFO or SC during the experiment. Least squares methods (SAS, 1995) were applied to each trait to find the most appropriate fixed-effects model. For calf traits up to 14 months of age, effects tested were those of line, contemporary group (year of birth by grazing group), age of dam, a covariate for date of birth within season, and two-way interactions. The two-way interactions were subsequently eliminated if accounting for less than ~3% of the sums of squares. For annual pregnancy rates of cows, the effects tested were those of line, year of birth and year of record, with a smaller model excluding year of record for cow lifetime traits involving joinings per lifetime and pregnancies per lifetime. For the annual pregnancy data, records were excluded when an animal was in a sub-fertile bull mating group with <60% pregnancy rate (Morris & Amyes, 2005). Results for all females when they were two-year-olds were adjusted for pregnancy status a year previously. The AFO data were transformed to an underlying scale, standardised age at first oestrus (SFO), with a standard deviation of unity, as if AFO was an ordered categorical response (Gianola & Norton, 1981). This was necessary because analyses to rank candidate sires were required part-way through the season when many heifer daughters still had not reached puberty. The standardisation process assisted with removal of some bias. Weight at first behavioural oestrus (WFO) was interpolated from monthly weights and first oestrus date. Age at puberty in bulls was interpolated (IAP) from serial SC data, using the American finding that pubertal age is closely predicted from the age at which they passed a threshold SC of 27.9 cm (Lunstra et al., 1978). Data on AFO, SFO, WFO, SC, IAP, pregnancy outcomes per female and all weights were available for all calf crops through to the end of the experiment, birth year 2007 and mating year 2007.

Restricted maximum likelihood (REML) procedures (Gilmour et *al*., 2002) were employed for genetic parameter estimates for AFO, SFO, WFO, SC and IAP, with an animal model and a full relationship matrix over all years of data combined, with pedigree back to 1979. The REML model for SC included repeated-animal terms for the monthly data. Breeding Values for SFO were used for selection decisions each year in both sexes. These came from a two-trait model with SFO and repeated-record SC. The 2005-born and later calves were measured for AP traits at Whatawhata, which is a hill country station with poorer grass growth than at Waikeria or Tokanui. Effects of site (Tokanui vs Whatawhata) on puberty traits were tested for the last seven years of data, by comparing line differences (Age+ mean minus Age- mean) at Tokanui (2001 to 2004) and at Whatawhata (2005 to 2007).

RESULTS

Long term responses

Phenotypic standard deviations for AFO, SFO, IAP and single-record SC were 52 d, 0.952, 38 d and 2.58 cm, respectively, after adjustment for fixed effects. Figure 1 shows the puberty responses achieved in the two selection lines alongside the Control line from 1985 to 2004, in yearlings recorded annually at the Waikeria and Tokanui sites for pubertal traits. Separation in SFO between the Age- and Age+ lines was achieved during the screening process in 1984/5, the year in which the lines were established. Through the early years of selection (1984/5 to 1991/2), which was applied to females only, there was limited divergence achieved, mainly in the Age- line. Following a second round of screening in 1992/3, where further separation between the lines was achieved, divergence continued from 1993 onwards with selection applied to both sexes, Selection on male records was applied via the genetic correlation between puberty traits in males and females. Averaging data for the 2003 and 2004 calf crops, the difference in age at puberty was 69 days, equivalent to 1.33 phenotypic standard deviations or 19% of the herd mean. Responses in heifer puberty were closely mirrored by responses in bull puberty, where the SC measurements in Age- bulls exceeded those in Age+ bulls for the 2003 and 2004 calf crops by 3.0 cm equivalent to 1.17 phenotypic standard deviations or 9.9% of the mean. The SC values were the means of measurements between eight and 13 months of age. The 13-month SC alone might provide a more familiar benchmark for bull breeders. This difference, in the 2003 and 2004 crops, averaged 3.2 cm or 9.6% of the mean. Heifers recorded at Whatawhata still showed a difference in AFO or SFO between lines, but these differences were smaller than at Tokanui (Figure 2).

Estimates of the annual rates of change in AFO in the Age+ and Age- lines were 0.77 ± 0.24 and -0.83 ± 0.31 d, respectively at Tokanui. Although these rates appeared symmetrical, the Control line was also negative, with an annual rate of -0.26 ± 0.48 d. The Control result was attributed to the genetic correlation between SFO and mean cow pregnancy rate, estimated as -0.23 ± 0.22 by Morris *et al*. (2000), in the early stages of this experiment. The culling of non-pregnant mixed-aged cows would make the SFO mean more negative in each line.

Yearling live weight of both sexes, was greater in the Age- than the Age+ line. Because of a significant interaction between year and line (P <0.05), the size of these line effects varied. For the 2001 to 2004 calf crops the Age- line was heavier by 10.8 ± 3.1 kg or 3.9% of the mean (P <0.001). For the 2003 and 2004 years, the difference was 6.8 ± 3.7 kg (P <0.07). Thus weights at fixed dates around the yearling stage were slightly greater in the Age- than the Age+ line. WFO was considerably lower in the Age- than the Age+ line by 16% or 47 ± 6 kg (P <0.001). See also Figure 2.

Environmental effect

After transferring all experimental stock from Tokanui to Whatawhata in June 2006, the 2005 and later calf crops experienced slower growth rates. As an example the heifers were 46 kg (18%) lighter at 12 months of age at Whatawhata than at Tokanui. Figure 2 shows the growth curves for Tokanui heifer calves (2001 to 2004 calf crops) and Whatawhata heifer calves (2005 to 2007). It also shows their mean dates at puberty, with selection line differences in AFO. These appeared to have diminished in the 2005 to 2007 calf crops when heifers experienced lower growth rates.

Genetic parameters

Realised heritability estimates for SFO and individual SC records up to 2004 were 0.26 ± 0.03 and 0.40 ± 0.04, respectively. The repeatability of SC over months between eight and 13 months of age was 0.68 ± 0.01. The SFO and SC data, obtained from the two-trait restricted maximum likelihood analysis, provided a realised genetic correlation estimate of -0.25 ± 0.089. Realised

FIGURE 1: Estimates of genetic change in standardised age at first oestrus in the selection and control lines, 1985 to 2004. Values back-transformed to age in days, by multiplying by 52, the phenotypic standard deviation of age at first oestrus.

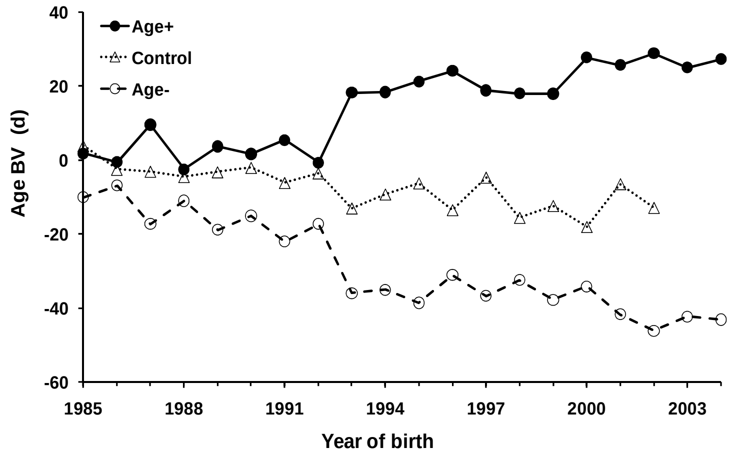
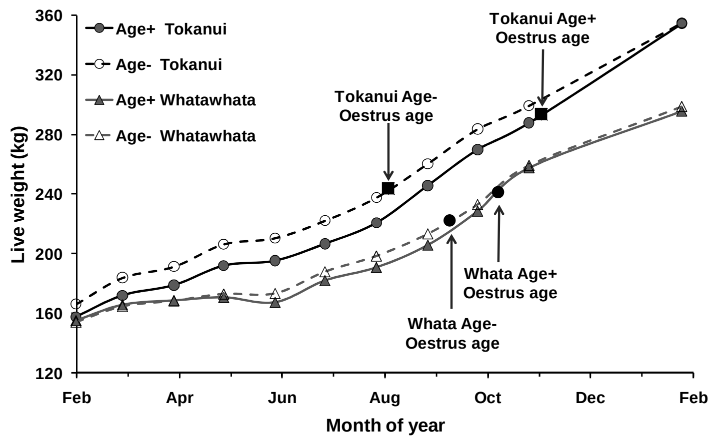


FIGURE 2: Mean monthly live weights of heifers in the 'Age-' and 'Age+' lines at Tokanui (2001-04 calf crops) and at Whatawhata (2005-07 calf crops), showing the mean date at first oestrus by line and site.



heritabilities for the associated pubertal traits of AFO, WFO and IAP, were: 0.25 ± 0.03, 0.42 ± 0.04 and 0.41 ± 0.05, respectively. Realised correlations between SFO and WFO in females were 0.75 ± 0.04 (genetic) and 0.73 ± 0.01 (phenotypic), and between pubertal age in the two sexes (SFO and IAP) 0.29 ± 0.10 (genetic).

From Figure 2, the fixed-time live weights in the two selection lines imply that the genetic correlation between heifer SFO and yearling live weight for age is negative, as was reported during the earlier stages of this experiment (-0.22 ± 0.09) by Morris *et al*. (2000).

Reproductive traits

Pregnancy rates, updated from values published up to 2003/4 (Morris *et al*., 2006), were greater in the Age- than Age+ selection lines across all ages of females. After removing data from sub-fertile bull mating groups, the pregnancy rate advantage to the Age- line was 26.0 ± 3.4 percentage points in yearlings, 12.2 ± 3.8 percentage points in two-year-olds and 2.2 ± 1.6 percentage points in three-year-old and older cows. Over all age groups this averaged a 10.3 ± 1.4 percentage point advantage to the Age- line, annually. On a lifetime basis for yearling heifers entering the herd, the Age- line had 1.01 ± 0.14 (39%) more joinings in the herd than Age+ heifers, and 0.87 ± 0.17 (29%) more pregnancies.

DISCUSSION

Long term responses

The second round of screening in 1992 achieved permanent separation between the lines, forming an important part of the total divergence of a 69-day difference in AFO by 2004. The annual rate of divergence in AFO from 1993 to 2004 was estimated at 1.60 days of age per year, with responses being equal and opposite for the Age- and Age+ lines. Relative to the Control line, however, the Age+ selection line was making faster progress because the necessary culling of non-pregnant cows, to prevent increases in herd numbers, appeared to produce an associated response in puberty. It was not possible to decide whether there is evidence of any slowing of the rate of divergence near the end of the trial because of a large apparent effect of site at Whatawhata for the 2005 to 2007 calf crops. The numbers mated per year remained stable in the Age-line, but the numbers mated in the Age+ line fell from an average of 117 cows and heifers per year in mating years 1996 to 1998. Initially this was to accommodate breeding contemporary back-cross cattle for a genomic study during the 1999 to 2002 mating years. Thereafter Age+ mating numbers averaged 76 cows and heifers per year.

Divergence rates of 0.19 ± 0.03 cm per year were achieved in average SC, and by 2004 there was a 3.2 cm (9.6%) difference in 13-month SC between the Age- and Age+ lines. This is a relatively easy measure to take, and is now commonly recorded in pedigree herds. Where Breed Association trends in SC are increasing, pregnancy rates should also be increasing genetically.

Environmental effect

With only three years of Whatawhata data available, there is no clear explanation for the result shown in Figure 2, where selection line differences in AFO at Whatawhata had diminished when heifers grew more slowly. It was not possible to re-estimate the heritability of SFO with 2005 to 2007 data only, because sires used were closely related within lines. Interpreting oestrous marks is slightly subjective, and different opportunities and constraints were involved at the two sites involving stockmen, topography and paddock size.

Genetic parameters

The heritabilities of SFO and AFO re-estimated in this study up to the 2004 calf crop were similar to those reported up to 1997 from earlier, more limited, data by Morris *et al.* (2000). They were also reasonably consistent, given the standard errors, with values for SFO and AFO from two separate beef cattle experiments carried out under New Zealand grazing conditions of 0.32 ± 0.10 and 0.33 ± 0.12, respectively (Morris *et al*., 1992) and 0.49 ± 0.09 and 0.34 ± 0.08 (Morris *et al*., 1993). Heritability estimates for SC are numerous. From http://www.gparm.csiro.au/, the average heritability for SC at fixed age, derived from 25 estimates, was 0.45. This is close to our value of 0.40 ± 0.04. Genetic correlations between heifer AFO and bull SC were estimated originally in the United States by Brinks *et al*. (1978) at -0.71, and by King *et al*. (1983) at -1.07. Lunstra *et al*. (1978) reported across-breed means of AFO plotted against SC at 7 and 10 months, giving a regression of -0.30 months of AFO in females per cm of SC in males of the same breed. Our genetic correlation was equivalent to a genetic regression of -0.13 months AFO per cm SC, whilst the actual rates of divergence between 1993 and 2004 were equivalent to a genetic regression of -1.60 days AFO per year for an SC change of 0.19 cm per year, or -0.28 months AFO per cm SC.

Reproductive traits

Probably the most important finding from this experiment was the favourable negative genetic correlation between heifer puberty age and mature cow pregnancy rate. The experiment also provided a demonstration of this correlation, in the form of differences between selection lines in annual pregnancy rates at all ages, and differences in lifetime survival time in the herd, favouring the Age- line. Similarly, Toelle and Robison (1985) reported that testicular measurements in yearling bulls had a favourable genetic correlation of 0.62 with pregnancy rates in female relatives. Other useful findings from the experiment include evidence of the ability to 'bend growth curves' by selecting on pubertal traits (Morris *et al*., 2006), where the Age- line was found to be heavier than the Age+ line up to about 24 months of age, but lighter for mixed-aged cows.

CONCLUSIONS

It is concluded overall that heifer and bull puberty traits are heritable, and it is possible to change them by selection. Reducing heifer AFO and increasing bull SC will lead to an increase in cow pregnancy rate.

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