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Correlated responses following genetic selection to change age at puberty in Angus cattle

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ABSTRACT

Direct and correlated responses in a 23-year selection experiment to change puberty in heifers are reviewed. Selection was for age at first oestrus (AFO). It was applied in both sexes, using the genetic correlation (-0.25 ± 0.09) between scrotal circumference in juvenile males and AFO in female relatives. The main breeding lines were those selected for early AFO (AGE-), late AFO (AGE+), or unselected (Control). A 69-day difference (19% of the herd mean) was achieved between the two AGE lines, with a 3.0 cm (9.9%) difference in scrotal circumference. Relative to the AGE+ line, the AGE- line means were $+10.8 \pm 3.1$ kg (3.9%) in yearling weight, -6.0 ± 3.0 kg (1.3%) in cow mature weight, -47 ± 6 kg (16%) in heifer weight at first oestrus, and $+3.7 \pm 1.5$ percentage points for mixed-aged cow pregnancy rate. There were significantly fewer sub-fertile yearling bulls in the AGE- line ($P < 0.001$), and maternal effects on autumn and winter weights on calves of this line were positive. For carcass composition, only depot fat differed significantly between lines (AGE- mean $<$ AGE+ mean). No major unfavourable traits were observed in the AGE- line in this study.

Keywords: puberty; cattle; selection; correlation; response.

INTRODUCTION

It is well known that pubertal traits in cattle are inherited. In females, three independent New Zealand estimates of the heritability of standardised age at first oestrus in beef cattle are: 0.32 ± 0.10 (Morris *et al.*, 1992), 0.49 ± 0.09 (Morris *et al.*, 1993a) and 0.26 ± 0.03 (Amyes & Morris, 2009), giving a combined value of 0.29 ± 0.03 . In males, Koots *et al.* (1994) reviewed heritability estimates of beef cattle traits including scrotal circumference (SC), reporting a mean estimate of 0.45 (25 values). A corresponding heritability estimate for SC was obtained from a summary of 25 estimates, with some from sources different from Koots, on the website of the Association for the Advancement of Animal Breeding and Genetics (http://www.gparrm.csiro.au/traits.html?sp_code=4&trt_code1=79; accessed 3 Dec. 2009), with an average value of 0.45 also. However, there has been only one multi-generation selection experiment to change puberty in cattle, namely the present experiment established and managed by AgResearch and its predecessors. It consists of an Angus herd where selection for puberty was maintained for 23 seasons with no outside introductions of genes. After three years of Angus line-crossing (1981/82 to 1983/84), the first round of selection in 1984/85 generated calves in winter/spring 1985. Various publications have provided updates of progress in the herd (Morris *et al.*, 1993b, 2000, 2006; Morris & Amyes, 2005; Amyes & Morris, 2009). This review attempts to combine all the correlated-response estimates from the study into a single summary. The study was able to provide measurements of realised correlated responses to selection, whereas published

analyses of other puberty studies can only provide genetic correlation data based on family relationships.

MATERIALS AND METHODS

Ethics

This work was carried out with the approval of the AgResearch Ruakura Animal Ethics Committee, Hamilton, New Zealand.

Animals recorded

Breeding objective

Age at first oestrus (AFO) was defined as the direct selection trait, and was selected from 1984/85 onwards. Selection for AFO was applied only in females during the early years of the study, and then in both sexes from 1992/93, using the known genetic correlation (-0.25 ± 0.09 ; Amyes & Morris, 2009) between SC in juvenile males and AFO in female relatives. The main breeding lines in the experiment were those selected for early AFO (AGE-), late AFO (AGE+), and an unselected (Control) (Morris & Wilson, 1997). The control line was discontinued after 2002/03.

Cattle recording and management

Selection lines of approximately 120 cows and a Control line of 90 cows were established in 1984/85. This was reduced from 1992/93 to between 70 and 100 cows per line. Generally 4 to 6 bulls were used annually per line for natural mating, except in the first eight years of the Control line, where a total of 37 bulls were used by artificial insemination. Details of cow and calf management were described by Morris and Wilson (1997) and Amyes and Morris (2009). Oestrus activity leading

to an oestrus date, and hence AFO, was monitored by staff about twice-weekly in heifers from eight to 17 months of age, with the assistance of tailpaint and paint marks from chinball-harnessed vasectomised bulls. During the mating period from 14 to 16 months of age, harness marks from entire bulls were used, sometimes also with tailpaint on heifers. SC was measured with a flexible tape on all bulls every month, from eight to 13 months of age. Cow culling was predominantly for non-pregnancy in cows three years old or more, and also based 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.

Statistical analyses

The AFO data were transformed and normalised for each calf crop, according to procedures proposed by Gianola and Norton (1981), to yield a standardised age at first oestrus (SFO), before further analysis. Age at puberty in males was interpolated at a SC of 27.9 cm, as described by Lunstra *et al.*, 1978. Data were analysed using least squares procedures in the SAS JMP (1995) package, adjusting for effects of year of birth, line, age of dam, grazing group, and with a covariate for date of birth within year. Animal-model restricted maximum likelihood analyses were also used (Gilmour *et al.*, 2002), with a repeated-record model for SC and the cow traits, to estimate heritabilities and genetic correlations among traits. A full relationship matrix was used, including all animals born in the trial, back to 1979. The fixed effects were similar to those in the least squares models, except that "line" was not required, because it was accounted for by the relationship matrix.

RESULTS

The realised heritability of SFO was 0.26 ± 0.03 . A difference in AFO of 69 days was achieved between the AGE+ and AGE- lines, representing 19% of the mean (Amyes & Morris, 2009). From those analyses, the phenotypic standard deviation of AFO was 52 days. Table 1 reviews the genetic correlations with SFO in the present experiment, for each productive, reproductive or carcass trait. In three cases with small numbers of records, only the line difference was estimated, with the sign given when it was significant. The realised responses (AGE- mean less AGE+ mean) in yearling weight, SC and mixed-age cow pregnancy rate estimated at the end of the trial were 10.8 ± 3.1 kg (3.9%), 3.0 ± 0.5 cm (9.9%) and $3.7 \pm 1.5\%$, respectively. Responses shown in Table 1 are scaled to that found with a 50-day AFO response. All three traits were

negatively correlated with SFO, and therefore they increased as AFO was reduced in the AGE- line, relative to the AGE+ line. Consistent with this, the Control line was intermediate between that for AGE+ and AGE- for each trait. SC was part of the index used to select replacement stock, but the other two traits were both dependant on genes associated with puberty. Age at puberty in males, calculated as an interpolated value, had a genetic correlation with SFO of 0.29 ± 0.10 (Amyes & Morris, 2009), indicating that pubertal age increased in a similar manner in both sexes, although selection was in one sex. The phenotypic correlation between SFO and yearling weight was estimated at -0.33 ± 0.02 . The genetic correlation between SFO and yearling weight in females was -0.25 ± 0.08 , whilst the genetic correlation between SFO and yearling weight from both sexes was similar to the above, at -0.33 ± 0.07 . To test for a possible correlated response in dystocia and calf deaths in two-year-old cows, as a result of puberty selection, the calf death rate during the first 24 hours after birth, was compared among lines. The overall mean death rate was 9.7% among calves of two-year-olds with no significant difference between lines.

Calculated responses measured from genetic regressions with other traits (Table 1) were obtained from parameter estimates of genetic correlations, realised heritabilities and standard deviations, mainly at time points before the end of the trial. The examples given refer to a 50-day change in AFO, equivalent to a 0.962 of a unit change in SFO. In the case of birth weight and weaning weight, both of which had direct and maternal components, combined responses were estimated in Table 1. Their responses were very small at these early stages of growth, but had the same sign as the yearling weight response. Weight at first oestrus was observed to be higher by 47 ± 6 kg (16%) in the AGE+ line than in the AGE- line which was scaled to be 34.1 kg higher for a 50-day difference in AFO. It was also predicted from the genetic correlation to be higher by a similar amount (30.3 kg) in the AGE+ than AGE- lines. For mature cow weights, there was a change in direction and in magnitude of predicted response, as the animals aged. The response was in the same direction as for yearling weight in females of one to four years of age (AGE- > AGE+), but this was reversed in older cows. Estimates of genetic correlations of SFO with cow mating weight by age were; one-year-olds (1yo), -0.65 ± 0.04 ; 2yo, -0.28 ± 0.08 ; 3yo, -0.19 ± 0.08 ; 4yo, -0.12 ± 0.09 ; 5yo, 0.04 ± 0.10 ; 6yo, 0.14 ± 0.11 ; 7yo, 0.25 ± 0.16 ; ≥ 8 yo, 0.15 ± 0.12 . Combining all age groups of five years and above led to a genetic correlation estimate for SFO with mating weight of 0.123 ± 0.059 ($P < 0.05$). The prediction for cow mating weight is shown in

TABLE 1: Genetic correlations of productive, reproductive and carcass traits with standardised age at first oestrus (SFO), and an example of the responses for these traits scaled to a 50-day increase in untransformed age at first oestrus (AFO). SD = Standard deviation.

Trait		Genetic correlation	SD	50-day AFO change (AGE+ less AGE-)	Reference
First oestrus age	Unstandardised (d)		52	50	Morris <i>et al.</i> (2000)
	Standardised (SFO)	1.00	0.96	0.96	Morris <i>et al.</i> (2000)
Measured responses at end of trial					
	Yearling live weight (kg)	-0.25 ± 0.08	21.5	-7.8	This publication
	Scrotal circumference ^a (cm)	-0.25 ± 0.09	2.4	-2.2	This publication
	Mixed-age cow pregnancy rate ^a (%)	-0.23 ± 0.22	35	-2.7	This publication
Calculated responses before end of trial					
Live weight	Birth (Direct) (kg)	0.21 ± 0.12	3.8	-0.24	Morris <i>et al.</i> (2000)
	Birth (Maternal) (kg)	-0.46 ± 0.13			Morris <i>et al.</i> (2000)
	Weaning (Direct) (kg)	0.07 ± 0.15	17.9	-1.31	Morris <i>et al.</i> (2000)
	Weaning (Maternal) (kg)	-0.11 ± 0.09			Morris <i>et al.</i> (2000)
	First oestrus (kg)	0.75 ± 0.04	32.3	30.3	Amyes & Morris (2009)
	Mating (1 to 4-yr-old) (kg)	-0.47 ± 0.03	36	-24.5	This publication
	Mating (>5-yr-old) (kg)	0.12 ± 0.06	46	7.4	This publication
Hot carcass (kg)	NS	16.5		Morris <i>et al.</i> (2006)	
Carcass pericardial fat (kg)	Positive	0.15		Morris <i>et al.</i> (2006)	
Bull fertility (%)	Negative			Morris & Amyes (2007)	
Calving date (d)	0.57 ± 0.17	13	4.2	Morris <i>et al.</i> (2000)	

^aSingle record SD is tabulated; response measured was based on multiple records.

Table 1. For comparison, average line differences measured each year over all ages were 4.4 ± 3.1 kg at mating, 6.0 ± 3.0 kg at weaning and 6.2 ± 3.9 kg for pre-calving weight, indicating heavier cows in the AGE+ than AGE- lines.

Carcass weights were similar in the two selection lines. Most composition traits did not differ between lines; however, pericardial, kidney and omental depot fat in the carcass were significantly reduced, especially pericardial fat, in the AGE- line, as reported by Morris *et al.* (2006).

For the remaining two reproductive traits in Table 1, the signs of their genetic correlations with SFO favoured the performance of the AGE- over the AGE+ line with a higher bull fertility and an earlier calving date. This was consistent with the data above: greater cow pregnancy rate and greater bull SC in the AGE- line.

DISCUSSION

Live weight

Growth from birth to maturity showed a pattern following selection which was consistent with the concept of “bending growth curves”: namely a relatively high yearling weight, but with little increase in birth weight, which could have led to increased dystocia, and a reduction in the mature cow weight. Carcass weights were similar in the two

selection lines. The slaughter age at mainly 20 to 21 months coincided with the period when the live-weight differences between lines were changing sign from the AGE+ line being lighter by 10.8 kg (3.9%) than the AGE- as yearlings, and heavier than AGE- in mature cows. Weight at first oestrus was lower by 47 kg (16%) in the AGE- than AGE+ lines, as expected from the existence of a large line difference in AFO, associated with only a small line difference in weight-for-age.

Maturity

This experiment has shown that single-trait puberty selection in the AGE- line has led to earlier sexual maturity but, according to the carcass fat data, minimal differences in chemical maturity. There was little or no difference in most composition traits between lines, although a slightly fatter AGE+ animal as shown with pericardial fat weight. Thus for a 69-day (19 %) reduction in AFO in the AGE- line and a corresponding 16% reduction in weight at first oestrus, the cue for expressing first oestrus was neither increasing fatness nor weight alone. Since the date for beginning mating was approximately the same each year in October, it is possible that the puberty cue may have included photoperiod and/or seasonal pasture growth. The selection lines may have become more or less sensitive to these cues; for example, circulating prolactin levels would have been expected to reflect

a photoperiod effect. This is currently under investigation with a genetic correlation of -0.29 ± 0.13 ($P < 0.05$) having been estimated in this herd between yearling log_e prolactin concentration and SFO (C.A. Morris, Unpublished data).

Reproductive rate

The mixed-age cow pregnancy rates were higher in the AGE- than in the Control line up to 2002/03 (Morris & Amyes, 2005), after which time the Control line was terminated. The AGE- line also had a higher mixed-age cow pregnancy rate than the AGE+ line. This was the reason Gary Bennett set up the experiment in 1984/85 with an original hypothesis to “monitor correlated responses in adult reproduction” (Morris *et al.*, 1993b). At the end of the trial, mixed-age cows in the AGE- line had a pregnancy rate that was $3.7 \pm 1.5\%$ greater ($P < 0.05$) than in the AGE+ line. These figures were adjusted to remove effects of sub-fertile bull groups with pregnancy rates $< 60\%$. There was a greater incidence of these sub-fertile groups in the AGE+ than in AGE- lines. Control-line pregnancy rates were in-between those of the AGE- and AGE+ lines, although the power of contrasts between the selection and Control lines was limited because of fewer Control cow numbers. Thus all four reproductive traits were favourably correlated with earlier AFO, namely greater pregnancy rate, earlier calving date, higher SC and reduced incidence of sub-fertile bulls.

ACKNOWLEDGEMENTS

We thank the Farm Managers and their staff at Tokanui and Whatawhata Stations for care of the stock, and for the collection of extensive field data. This research was funded by the New Zealand Foundation for Research, Science and Technology.

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