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Phenotypic response to mass selection for weaning weight and 18-month weight in Tswana cattle

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The objectives of this study were to identify the environmental factors that influenced growth traits and to evaluate phenotypic response of growth traits to selection at weaning (S1) and 18 months of age (S2) in Tswana cattle. Phenotypic analysis for average daily gains (ADGs) and growth traits were conducted using 7226 records of animals, which were born between 1995 and 2013 from 1662 dams and 188 sires in 54 contemporary groups, using mixed models. Growth traits analysed were birth weight (BWT), weaning weight (WWT), yearling weight (YWT) and 18-month weight (EWT). The analysed ADGs were pre-weaning average daily gain (ADG1) and post-weaning average daily gain (ADG2). The identified significant environmental effects for growth traits and ADGs were sex of the animal, dam age, selection line and contemporary group. S1 resulted in increased BWT, WWT, YWT, EWT and ADGs compared with S2. Animals from both S1 and S2 exhibited higher weights and ADGs than those in the unselected control line (S3). The significant environmental factors should be accounted for whenever genetic evaluation for growth performance of Tswana cattle breed is carried out. Mass selection for weaning weight can yield optimal improvement on growth performance of Tswana cattle when properly carried out.

Key words: Environmental factors, growth performance, growth traits, cattle, selection.

INTRODUCTION

Tswana cattle breed is distinctly adapted to the harsh environment of the Southern African region. However, profitability from its farming is limited by biological and socio-economic factors. The market weight of Tswana cattle at weaning, yearling and eighteen months of age is inferior to that of other local beef breeds, pure exotics and their crosses (APRRU, 1999). As a result, the breed has been overlooked by commercial farmers, although the majority of subsistence farmers have always given preference to it. The most limiting factor to the improvement of Tswana cattle has been a lack of proper research on strategies that can be employed, as well as parameters associated with their production performance. It was on this basis that a two line mass selection project, that is, selection for weight at weaning and at eighteen months of age using phenotypic index, was set in 1995 at

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Table 1. Pedigree structure for the data used.

Parameter	Selection line		
	1	2	3
Number of animals	2940	3034	1252
Number of dams[a]	731	671	266
Number of sires[a]	80	82	31
Contemporary group	54	54	54

[a]Sires and dams with progeny records, selection lines 1, 2 and 3 are selection for weaning weight, 18-month weight and unselected control population, respectively.

the Department of Agricultural Research (DAR) in in Botswana (APRRU, 1999). The project has since generated a reasonable amount of data and the current study attempted to utilize this data to provide guidance on the future breeding objective for Tswana breed.

Selection of animals for growth traits has proven to result in enhanced growth performance (Kahi and Hirooka, 2007; Bennett et al., 2007; Enns and Nicoll, 2008). In addition to that, McHugh et al. (2014) asserted that genetic evaluations provide information to aid in breeding decisions that increase long-term performance of animals and herds. Furthermore, growth traits of animals are determined by both genetic potential and environmental influence as Koch et al. (2004) described. As a result, accurate genetic evaluation can be achieved by adjusting animal records for known systematic environmental effects, such as individual age differences at recording, sex, dam age, year and season (Bohmanova et al., 2005). The objectives of this study were: (1) to identify the environmental factors that influenced growth traits and (2) to evaluate phenotypic response of growth traits to selection at weaning and 18 months of age in Tswana cattle.

MATERIALS AND METHODS

The experimental ranch covered an area of about 6628 ha with the recommended stoking rate of about 10.3 ha/Lsu and receives the annual rainfall ranging from 212 to 710 mm. The soil types are non-calcareous fine sandy soils with the vegetation dominated by woody plants species such as *Dichrostachys cinerea, Terminalia sericea, Acacia hebclada, Diospyros lycioides* and *Grewia flava* which are mostly known as encroacher plants, however the ranch condition has been largely characterized as fair in terms of pasture production due to high presence of palatable grass species such as *Digitaria, Cynodon dactylon, Brachiaria nigropedata, Schimidtia pappophoroides* and *Urochloa trichopus*, which are either increaser I or decreaser species, and their abundance was said to suggest fair utilization. Animal were allowed to graze on natural pasture in a ranch for the better part of the year and only supplemented during dry seasons such as winter or drought periods following years of low rainfall. The mineral supplementation was done using dicalcium phosphate.

Three months breeding season starting from January 1st to March 31st was practiced while calving season was from late September to early January every year. Bulls were separated from the cows at the end of the breeding season. Pregnancy diagnosis was conducted in June (three months after breeding season ends) every year. When cows were in their last months of pregnancy, they were brought near the handling facilities for observation and assistance when the need arise. Upon birth of new calves, birth weight and date, dam and sire identity, sex and colour of the calf, cow's previous parous status were recorded. Cows and calves were weighed within 24 h of calving. All calves were ear tagged and given identity numbers at first weighing and then allowed to receive all the milk from their dams until they were weaned. Monthly weighing of all livestock was a routine procedure performed on the 15th day of every month. At about 7 months of age, calves were weaned and branded. Calves were then separated and females remained in the heifer herd until ready for selection into the breeding herd. After selection for replacement stock, excess heifers and bulls were sold on auction to local farmers for breeding while those that did not meet selection desires were culled.

The government through Ministry of Agriculture (MoA) was responsible for the prevention and control of economically important diseases such as foot and mouth, anthrax, botulism and black quarter or quarter evil. Animals were routinely vaccinated by the Department of Veterinary Services (DVS) and in some cases by project technical staff.

Data of selected Tswana cattle collected over a period of 18 years from 1995 to 2013, acquired from the Department of Agricultural Research (DAR) in Botswana was used in this study. The data was edited for missing records such as birth and weaning dates, weight traits and pedigree information. The final data consisted of 2940 records for weaning weight (7 months) selection line (S1), 3034 for 18 months selection line (S2) and 1252 records for the unselected control line (S3). In both S1 and S2, mass selection was practiced based on the animal's weight index. The weight indices were derived as the difference between the animal's own weight record for a trait and the average weight of the contemporary group. Therefore, before the indices were calculated on both weaning and eighteen-month weights, weight records were pre-adjusted to 205 and 540 days of age, respectively, to eliminate the differences in individual age within contemporary group. S1 and S2 replacement animals were then selected using 205 and 540 days weight indices, respectively, while S3 replacement animals were randomly chosen into the breeding herd at eighteen months of age, without using any distinct (random) selection procedure. All the animals were allowed to join the breeding herd at 18 months of age. All animals with unknown birth date, sire or dam were discarded. The final data comprised the following: pedigree information, that is, calf identity number, sire identity number, dam identity number and associated important information, such as birth date, sex of the calf, and selection line. The pedigree structure showing the number of animals, dams and sires for each line is shown in Table 1.

Growth traits consisted of birth weight (BWT), weaning weight (WWT) recorded at seven months of age, yearling weight (YWT) recorded at 12 months of age, 18-month weight (EWT), pre-weaning average daily gain (ADG1) and post-weaning average daily gain (ADG2). ADG1 was calculated by dividing the change in

Table 2. Least square means (± S.E.) for BWT, WWT, YWT, EWT, ADG1 and ADG2 by calf sex.

Sex	Trait					
	BWT (kg)	WWT (kg)	ADG1 (kg/day)	YWT (kg)	EWT (kg)	ADG2 (kg/day)
F	30.7±0.19[a]	157.7±2.63[a]	0.61±0.01[a]	160.3±2.94[a]	211.5±3.64[a]	0.16±0.01[a]
M	32.5±0.19[b]	168.9±2.63[b]	0.65±0.01[b]	172.5±2.95[b]	224.6±3.69[b]	0.18±0.01[b]

F=Female, M=Male, BWT=birth weight, WWT=weaning weight, YWT=yearling weight, EWT= eighteen month weight, ADG1=pre-weaning average daily gain, ADG2=post-weaning average daily gain. [a,b]Means within a column with different superscript are different (P<0.05).

body mass from birth to weaning by the age (in days) of the animal at weaning, while ADG2 was calculated as the change in body mass from weaning to eighteen months of age divided by the number of days in the interval.

In this study, the dam age was fitted as a fixed categorical variable after grouping the dam age into three classes: dams aged less than 5 years were grouped to form class 1, those aged greater than 5 to 9 years were grouped to form class 2, while those aged older than 9 years formed class 3. Weaning, yearling and eighteen-month weights were pre-adjusted to 205, 365 and 550 days of age, respectively; therefore, individual age difference at recording was not fitted as an effect in the analysis model.

Since seasonal mating was practiced, all animals were born from late September to early January; hence, there were fewer birth records in September and January than in October, November and December. As a result, the birth months were regrouped as follows: September and October were grouped as season 1, November as season 2, and December and January as season 3. After regrouping the birth month, contemporary group was then formed by concatenating birth year and birth season. All contemporary groups with less than 5 animals were discarded. The contemporary group was fitted as random effect in a mixed model.

Estimation of least square means for birth weight was carried out by fitting selection line, sex and age of dam as fixed class variables, and contemporary group as a random effect. The fixed and random effects fitted for weaning weight, post-weaning weights, ADG1 and ADG2 were similar to those fitted for birth weight. For all traits, the significant interaction effects were sex by contemporary group and selection line by contemporary group.

Data for all the traits were analyzed using PROC MIXED of Statistical Analysis System (SAS, 2012). The general form of the mixed models fitted for birth, weaning, yearling and 18-month weights as well as ADGs was as follows:

$$Y_{ijklm} = s_i + d_j + l_k + c_l + (s{\times}c)_{il} + (l{\times}c)_{kl} + e_{ijklm}$$

where Y_{ijklm} is the observation of the weight trait (BWT, WWT, YWT, EWT, ADG1 and ADG2), s_i is the i^{th} sex of the calf effect fitted as fixed, d_j is the j^{th} dam age class effect fitted as fixed, c_k is the k^{th} contemporary group effect fitted as random effect, l_l is the l^{th} selection line effect fitted as fixed, $(s{\times}c)_{il}$ is the sex by contemporary group interaction fitted as random effect, $(l{\times}c)_{kl}$ is the selection line by contemporary group interaction fitted as random effect, and e_{ijklm} is the random residual error, distributed independently with mean zero and common variance, σ^2_e.

RESULTS AND DISCUSSION

Least square means for all growth traits by sex are shown in Table 2. The sex of the calf was generally a significant source of variation in all weights and ADGs. The magnitude of the differences between the sexes in weight traits increased as the age of the animals advanced from birth (1.77±0.15 kg) to eighteen months (13.06±1.69 kg). Mean differences between males and females were 0.05±0.003 and 0.02±0.002 kg for ADG1 and ADG2, respectively, and were both significant. The higher male ADGs imply that male calves grow faster than their female counterparts both prior to weaning and from weaning to eighteen months of age. The results of the current study are in agreement with the findings reported by both Irgang et al. (1985a), for Hereford cattle, and Casas et al. (2011), for British and indigenous tropical beef breeds. Contrary to the values obtained in the current study for ADG1, Casas et al. (2011) reported higher ADG1 values, ranging from 0.93±0.1 to 1.0±0.1 kg/day for crossbred calves sired by Tuli, Boran and Brahman bulls in temperate climate.

It is well documented that male calves are heavier at all stages of growth than their female counterparts and the differences have been detected regardless of breed (Bellows et al., 1996; Cundiff et al., 1998; Chase et al., 2000; Holloway et al., 2002; Riley et al., 2007). Birth weight mean difference of 1.77±0.15 kg obtained in this study between the two sexes was consistent and within the range of values (1.4±0.5, 1.72 and 2.4 kg) reported for indigenous tropical beef cattle breeds (Dillon et al., 2015; Robinson et al., 2013; Tubman et al., 2004). However, these values are lower than the range of values (2.74±0.11 to 3.73±0.14 kg) reported by Bennett et al. (2007) for European beef breeds. Likewise, Casas et al. (2011) also reported differences ranging from 2.2 to 3.1 kg between female and male calves for crossbred calves from Hereford, Angus, Tuli and Belgian Blue sires. Differences between weights of male and female calves were also reported by Smith et al. (1976), Gregory et al. (1978,1979), and Cundiff et al. (1998), and may be attributed to physiological differences arising from sex linked secondary characters.

Mean weight differences obtained between male and female calves were 11.25±0.53, 12.28±1.34 and 13.06±1.69 kg in WWT, YWT, and EWT, respectively. Weaning weight differences obtained in this study were consistent with the findings by Chase et al. (2004) and Casas et al. (2011), who as well observed the persistence of sex effect from birth to weaning. In addition, Irgang et al. (1985c) also reported sex effects at weaning and post-weaning while evaluating lines selected for both weaning

Table 3. Least square means (± S.E.) for BWT, WWT, YWT, EWT, ADG1 and ADG2 by dam age.

Trait	Dam age category (years)		
	≤5	>5 and ≤9	>9
BWT (kg)	31.0±0.19[a]	32.9±0.19[b]	31.9±0.20[b]
WWT (kg)	156.7±2.64[a]	167.3±2.64[b]	165.9±2.66[c]
ADG1(kg/day)	0.60±0.01[a]	0.65±0.01[b]	0.64±0.01[c]
YWT (kg)	161.7±2.90[a]	169.3±2.90[b]	168.1±2.92[b]
EWT (kg)	212.9±3.61[a]	221.7±3.61[b]	219.5±3.63[b]
ADG2 (kg/day)	0.17±0.01[a]	0.17±0.01[a]	0.16±0.01[a]

BWT=birth weight, WWT=weaning weight, YWT= yearling weight, EWT= eighteen-month weight, ADG1= pre-weaning average daily gain, ADG2= post-weaning average daily gain. [a,b,c]Means within a row with different superscript are different (P<0.05).

weight and post-weaning gain. Furthermore, the results obtained by Luna-Nevarez et al. (2010) in their study of associative relationship between growth characteristics and reproductive performance also revealed females to be lighter than males at weaning and yearling, and weight differences became large as the age of animals advances. This may be due to the development of secondary male sexual characteristics such as production of testosterone, which helps build the muscle hence increase body frame in males. However, this effect has not resulted in heterogeneous variance components (Demeke et al., 2003; Casas et al., 2011; Kim and David, 2013). It is therefore necessary to adjust for sex effect whenever genetic evaluation of Tswana cattle for growth performance is carried out.

Least square means for birth, weaning, yearling and eighteen-month weights and pre- and post-weaning average daily gains by dam age categories are shown in Table 3. The mean weight differences between calves born from young dams aged 5 years or less and those born from mature dams aged above 5 to 9 years were 0.84±0.14, 10.96±0.64, 7.61±0.82 and 8.83±1.04 kg for BWT, WWT, YWT and EWT, respectively, while the corresponding mean differences between calves born from young dams and older ones aged above 9 years were 0.85±0.15, 9.29±0.68, 6.40±0.89, and 6.58±1.12 kg for BWT, WWT, YWT and EWT. All differences were significant. However, differences between calves born from dams older than 9 years and mature ones ranged from 0.01±0.15 for BWT to 2.25±1.10 kg for EWT, and were not significant (P>0.05), except for weaning weight, which was significant. The results revealed ADG1 mean differences to be significant across dam age categories and were 0.04±0.003 kg/day between young and older dams, 0.05±0.003 kg/day between young and mature dams, and 0.01±0.003 between mature and older dams. ADG2 mean differences were not significant (P>0.05) across dam age categories and ranged from 0.003±0.003 kg between young and mature dams to 0.006±0.003 kg between older and mature dams. The means for both ADG1 and ADG2 are shown in Table 3.

The results obtained in the current study indicated that BWT, WWT, YWT and EWT of calves increased with dam age. Calves born from dams older than 5 years had the heaviest weight at all ages compared to those born from younger dams (Table 3). These results are in agreement with the findings reported by Irgang et al. (1985b), Bennett et al. (2007), BIF (2010) and Luna-Nevarez et al. (2010). These authors also observed increases in birth, weaning and yearling weights with dam age. Similar to the results obtained in the current study, Irgang et al. (1985a) and Bennett et al. (2007) also reported weaning and yearling weights that increased with dam age up to 5 years. However, contrary to the current findings, the authors revealed that the weights remained constant beyond 5 years of dam age. Furthermore, Luna-Nevarez et al. (2010) reported significant (P<0.05) dam age effect on birth weight of Brangus cattle and they revealed that birth weight increased with dam age up to 5 years, which was similar to the current findings. In addition to that, the authors further stated that the weights remained constant after 5 years until 11 years, then declined, which was inconsistent with the current results.

The observed weight and growth rate differences with dam age imply that young dams are unable to provide adequate uterine and nutrient environment for growth of the foetus during pregnancy and after birth to weaning (Dillon et al., 2015). This may be due to the fact that young dams are still growing hence the uterus is not yet fully developed, and besides that the nutrients supplied are partitioned not only for lactation and maintenance but also for the dam's own growth. Despite the ability of Tswana dams older than 9 years to provide adequate prenatal environmental requirements for the growth of foetus, they fail to provide sufficient environmental needs for postnatal growth of calves to weaning. This may be attributed to loss of efficiency of the digestive system to mobilise feeds consumed and supply enough nutrients for lactation, maintenance and repair of the worn out

Table 4. Least square means (± S.E.) of BWT, WWT, YWT and EWT for selected and control lines.

Selection line	Trait					
	BWT (kg)	WWT (kg)	YWT (kg)	EWT (kg)	ADG1 (kg/day)	ADG2 (kg/day)
S1	32.0±0.22[a]	171.5±2.88[a]	174.9±3.22[a]	231.3±4.30[a]	0.67±0.01[a]	0.19±0.01[a]
S2	31.7±0.22[b]	166.2±2.88[b]	169.7±3.21[b]	218.2±4.29[b]	0.64±0.01[b]	0.16±0.01[b]
S3	31.1±0.24[c]	152.3±2.92[c]	154.7±3.27[c]	204.6±4.33[c]	0.58±0.02[c]	0.15±0.01[c]

S1=animals selected at weaning, S2= animals selected at eighteen months of age, S3= unselected animals (control), BWT=birth weight, WWT= weaning weight, YWT= yearling weight, EWT=eighteen-month weight, ADG1=pre-weaning average daily gain, ADG2= post-weaning average daily gain. [a,b,c]Means within a column with different superscript are different (P<0.05).

tissues (Assan, 2013; Boligon et al., 2013).

Generally, the current results for ADG1 implied that calves born from young and older dams grow more slowly than their counterparts born from mature dams. The results obtained in the current study are consistent with the findings of Bennett et al. (2007) and Luna-Nevarez et al. (2010). However, the values obtained by Bennett et al. (2007), which ranged between 0.82 and 0.97 kg for pre-weaning average daily gain of different cattle populations, were higher than those obtained in the current study. Variation of ADG1 with dam age may be due to the inability of both young and older dams to provide sufficient nutrients for their own growth and repair of worn out tissues, respectively, coupled with those required for lactation, hence less milk produced for their suckling calves. The dam age effect was not significant for ADG2 and the average growth rate obtained for this period is much lower than that reported by Salimi et al. (2017). Similar to ADG1, the means obtained for ADG2 by dam age in this study were lower than the values reported by Bennett et al. (2007) for different beef cattle breeds, which were in the range of 0.95 to 0.97 kg.

Although most studies reported dam age effect on birth and weaning weight traits as compared to post-weaning growth traits, few literature findings (Bennett et al., 2007; Raphaka and Dzama, 2010) reported significant dam age effect on yearling and eighteen-month weights. In general, similar pattern of dam age effect was observed in the current study, in which the effect persisted beyond weaning age. These results indicate that for accurate genetic evaluation to be performed on both pre-weaning and post-weaning growth performance of Tswana cattle, adjustment for dam age should be taken into consideration.

Least square means for BWT, WWT, YWT, EWT and ADGs of selected and control lines are shown in Table 4. Both selection lines (S1 and S2) had significantly heavier weights at all ages than the control line (S3). Weight differences also varied significantly between the two selected lines and ranged from 0.28±0.24 to 13.04±4.15 kg at birth to 18 month olds. The highest mean weight differences were observed between animals in S1 and the control group for all growth traits and ranged from 0.96±0.27 to 26.66±4.22 kg at birth to eighteen-month olds. The mean difference between animals in S2 and S3 were 0.68±0.27, 13.83±2.14, 14.90±2.61 and 13.61±4.20 kg for BWT, WWT, YWT and EWT, respectively. The least square means for ADG also showed variation (P<0.001) with selection line (Table 4). The respective mean differences for ADG1 and ADG2 were 0.08±0.01 kg/day and 0.04±0.003 kg/day between animals in S1 and S3, 0.06±0.01 and 0.01±0.003 kg/day between animals in S2 and S3, and 0.02±0.01 and 0.03±0.003 kg/day between animals in S1 and S2.

The results for growth traits comparison between selection lines obtained in the current study are in agreement with other findings (Irgang et al., 1985b; Koch et al., 2004; Kahi and Hirooka, 2007; Bennett et al., 2007; Enns and Nicoll, 2008) in that the selected lines were heavier than the control line. However, contrary to the current results, Irgang et al. (1985c) reported that improvement on weaning weight, yearling weight and post-weaning gains were achieved by male calves due to selection for post-weaning gain than for selection on weaning weight. Likewise, Koch et al. (2004) also found animals selected for yearling weight to be heavier than those selected for weaning weight at both weaning and yearling age. The same authors also reported that both selected lines were heavier than the control line at both weaning and yearling. In general, compared to the unselected control populations, calves selected at weaning had the heaviest weight at all ages than those selected at eighteen months of age, which is in contrast to what has been reported (Irgang et al., 1985c; Koch el al., 2004; Kahi and Hirooka, 2007; Bennett et al., 2007; Enns and Nicoll, 2008; Boligon et al., 2010; Boligon et al., 2013).

Weaning weight is associated with the ability of the cow to provide the necessary environmental requirements in the form of milk and care for the calf to grow efficiently, while eighteen-month weight is said to be dependent on the animal’s own ability to grow, hence is influenced by the animal’s own genetic makeup (Anon, 2004; Boligon et al., 2010; Boligon et al., 2013). The current results indicated that selecting for weaning weight indirectly improved both yearling and eighteen-month weight, which is associated with the animal’s ability to grow independently of maternal environmental influence.

Therefore, the current results implied that the animal's genes responsible for good mothering ability may be the same genes or highly linked with the genes accountable for post-weaning growth performance.

Similar to the current results, Irgang et al. (1985b) and Koch et al. (2004) reported ADG means for selected populations that were high and significantly different from those of non-selected control populations. Bennet et al. (2007) also reported pre-weaning ADG that was significantly increased by selection for postnatal growth, while post-weaning ADG remained similar to that of the non-selected control population. The results obtained for both ADG1 and ADG2 in this study generally showed lower estimates than those earlier reported (Bennett et al., 2007; Luna-Nevarez et al., 2010; Casas et al., 2011), which may explain the low growth rate of Tswana cattle breed. The current results imply that selection for weaning weight has the potential to effectively improve growth rate in Tswana breed.

Conclusion

The study revealed that mass selection for weaning and eighteen-month weights based on phenotypic weight index improved the phenotypic growth performance of Tswana cattle compared to unselected control population. Selection for weaning weight resulted in heavier birth, weaning, yearling and eighteen-month weight traits and higher ADGs than selection for eighteen-month weight. Both calf sex and dam age have significant influence on all growth traits in Tswana cattle, and should be accounted for whenever genetic evaluation for growth performance of this breed is carried out. Therefore, it can be concluded that mass selection for weaning weight can yield optimal improvement on growth performance of Tswana cattle breed when properly carried out.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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